Ecology and Ethno-ornithology of Black Kites *Milvus migrans* in Delhi, India

Thesis submitted for the degree of Doctor of Philosophy

Michaelmas Term 2018 -19



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This thesis is dedicated to the numerous citizens of the societies in the developing countries, where religiously ascribed empathy and cultural expressions to the animal species in a shared ecosystem need equal (if not more) conservation attention.

(Below, I mention a quintessential verbatim)

मेरे पास गिद्धों, एवं बाकी पक्षियों) के विलुप्त हो जाने के दुःख को बयां करने के लिए शब्द नहीं हैं मैं बस इतना कह सकता हूँ, कि आस-पास के जीवों के लुप्तप्राय होने पर)ठीक वैसा ही महसूस होता है, मानो कोई अपना गुज़र गया हो।

आप उस दर्द का इज़हार शब्दों में नहीं कर सकते!

I have no words to describe the feeling, having witnessed the local extinction of vultures and many other species of birds. If I try, I can only equate this loss with the death of someone close.

You can't describe (model) the grief in words!

DECLARATION

I, hereby, declare that this dissertation, titled, "Ecology and Ethno-ornithology of Black Kites *Milvus migrans* in Delhi, India", constitutes original research conducted by me under the supervision of Prof. Andrew G. Gosler, faculty member at the University of Oxford, and Dr. Fabrizio Sergio, faculty member at the Doñana Biological Station, CSIC; Spain. The thesis has been submitted to the University of Oxford for the award of the degree of Doctor of Philosophy in Zoology, and has not formed the basis for the award of any other degree. It embodies my own work and observations; and in that respect, the investigation advances knowledge on the subject.

Nishant Kumar (D. Phil. Candidate)

Place: Oxfordshire Date: 11.01.2019

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ACKNOWLEDGEMENTS

I would like to thank my supervisors, Dr. Andrew Gosler and Dr Fabrizio Sergio for their guidance and support. This study began in a very nurturing mentorship of Dr. Fabrizio Sergio, Prof(s). Y V Jhala and Q Qureshi, effectively leading to a M.Sc. dissertation in 2012-13. The preliminary inferences paved way for a long-term inquiry (Black Kite Project is running through its fifth phase: 2018 to 2020), beginning with a doctoral dissertation in 2014. My D. Phil. advisory committee members Prof(s) Y. V. Jhala, Qamar Qureshi, Tom Pizzari and Chris Perrins are acknowledged for their valuable inputs. Faculty members, friends and colleagues at the Edward Grey Institute, Somerville College, and the Wildlife Institute of India are acknowledged for crucial and thoughtful discussions. Dr. Alessandro Tanferna, Prof. Ben Sheldon and Prof. B Harriss-White helped, and provided guidance on research aspects. I would like to thank the trustees, members and advisors of the Felix Scholarship Trust, Somerville College, Raptor Research and Conservation Foundation, Mumbai, Microwave Telemetry USA, Edward Grey Institute and WII for funding and supporting the project. Special thanks to R. Naoroji, K. Srivastava, Kim Ooi, Dr. Franz Kuemmeth and Marc Buentjen for constant support. Dr. Fabrizio also aided the project with biologgers and other equipment, afforded from the multiple grants: Project RNM-7307 of the Junta de Andalucía and CGL2015- 69445-P of the Spanish Ministry of Economy and Competitiveness. My project supervisors from WII aided the fieldwork with trail cameras, binoculars, handheld GPS units, etc.

I would also thank Ujjwal Kumar, and the Director, Dean and research coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Delhi Transport Corporation, Civic bodies of the Government of NCT of Delhi helped with legal permits, and the Director of the National Zoological Park of New Delhi gave access to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We express our most heartfelt gratitude to more than 100 researcher, interns and volunteers of the "Black Kite Project Group" from WII, University of Delhi (Sri Venkateswara and Deshbandhu Colleges), especially U Gupta, H. Malhotra, A. Singh, P. Kumar, Y. Taneja, M. Kalita, A. Mehta, M. Singh, Rubina, Urjaswi and N Kumar, who provided essential field help,

enthusiasm and cooperation in the environmental education of locally assembling crowds of curious people. Special thanks to our field assistants Laxmi Narayan, Prince Kumar and Poonam, who were the backbone of the field team. Finally, thanks to all the landowners, managers and government officials who patiently cooperated with our constant requests of access.

My heartfelt gratitude shall go all the well-wishers: support staff at OxZoo (Heather, Lynne, Sharon, Caitlin, Reception Staff, IT Zoology, Alexander Library, Darwin's), Somerville (Potter's lodge, Academic Office, Senior Tutor, College Tutors), WII (Tiger Cell, academic and administrative staff, library staff, dining hall, other support staff), families of my supervisors, and at various institutions in Delhi for taking keen interest in my study, and offering all the possible help. No words can ever express my gratitude to my own family members (especially my siblings) who are pillars of my strength. Lastly, thanks to the birds and citizens of Delhi. Researching this system has been so enjoyable!

Abstract

Rapid worldwide urbanization is generating a steep growth in studies on urban ecology, but tropical cities have had extremely scarce attention. To fill this gap of knowledge, in this thesis, I studied a dense population of an avian predator and facultative scavenger, the Black Kite Milvus migrans, breeding within Delhi, a 16million-inhabitants megacity. I studied the ways in which this species managed to adapt, respond and exploit such an extreme urban environment by running analyses at individual as well as population-level, through sampling at 28 independent plots, stratified and (randomly) scattered, to cover all the urban configurations present in Delhi. In particular, I focused on the dependence of this population on anthropogenic subsidies, afforded as human waste (in the streets or at refuse tips) and as intentional "ritual offerings" of meat scraps for religious purposes, especially by people of Islamic faith that are concentrated in "Muslim settlements". I found that the kite breeding population was stable over the past five decades, with a diet strongly dominated by human subsidies, especially ritual offerings, and with an extremely high density that makes it the largest raptor concentration of the world. Kites were not randomly distributed in the city but over-selected areas with high human density, poor waste management and a road configuration that facilitated ready access to resources provided by humans, in particular to Muslim colonies that provided ritual subsidies. Rather than a nuisance to avoid, as previously portrayed, humans were thus a keenly-targeted foraging resource. These individual-level preferences translated into population-level effects, with kite density tightly tied to Muslim subsidies. This relationship was further modulated by nest-site availability, mainly in the form of tree availability, which paved the way to potential population-manipulation through tree management. Ecological responses were accompanied and mediated by behavioural adjustments to the urban gradient, which not only provided adaptive benefits but also generated potential conflicts with humans. In particular, offspring defence was finely-tuned on human subsidies, probably as a result of the associated parental investments and familiarity with humans. In its most extreme form, nest defence led to attacks on humans, sometimes with serious physical harm. I show that such aggression was tied to frequent exposure to humans by kites while accessing their ritual subsidies and by constant close proximity to them while breeding, as caused by local architecture (balconies in the immediate proximity of nests). Despite the conflict, I also report the extremely benevolent attitudes of local people to the attacking kites, typical of southern-Asian cultural beliefs, but extremely unusual for western urban standards. Finally, I show how the stunning predator densities observed in Delhi are generated by the local breeding subspecies, but also by thousands of Black-eared Kites of the migratory M. m. lineatus subspecies that settle in Delhi during their wintering, non-breeding period. Through GPS-tagging, I found that they migrate to Delhi from their breeding quarters of Russia, Kazakhstan, China and Mongolia through a 3300-4700 km migration in which they regularly cross the Himalaya range at elevations of up to 5000-6000 m a.s.l., an aspect hitherto unknown. I discuss all my findings in terms of their contribution to broadening our views of urban ecology so that it is more inclusive of patterns and processes that better characterize the tropical cities of non-western nations. In particular, all my results stress the overriding importance of incorporating human socio-cultural factors in urban ecological studies.

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3 Appendix [Typescript Journal Articles (6) and two Comic Booklets in *English* and *Hindi*]

General Introduction

Urbanization has achieved a major landmark in its history with the majority of people now living in cities (United Nations, 2014). Despite well recognised threats of rapid urbanisation to biodiversity, there remains a paucity of ecological studies from tropical megacities. These cities are supposed to face the burden of persistent and steeply growing urbanization over the coming decades. This problem takes on yet further dimensions in the context of ever increasing technological changes (e.g. over ground power transmission line networks, mobile towers, wind turbines, high rise buildings with intense lights, etc.). Rapid urban sprawl has consequent impacts on the energy flow and nutrient cycles of urban ecosystems, which further get accentuated by a rise in the built up area and habitat degradation (e.g. McKinney, 2010; Pickett et al., 2001).

A wide variety of organisms, and many birds, have co-existed with humans for centuries as urban exploiters or *anthropo-dependent* commensals (Hulme-Beaman et al., 2016). However, a subtle oversight regarding effect of increased urbanization is reflected in the changing direct and indirect contact these 'citizens' have with nature, as cities becomes sinks to the immigrating humans from the rural areas (Crane & Kinzig, 2005). As a long-term effect, it is likely that socio-cultural shifts will increase urban-versus-rural disagreement on priorities for backyard biodiversity. This disagreement is even further reflected in urban political ecology which factors decisions constituting 'appropriate' wildlife or habitat management. While urban ecological research has already investigated various selection pressures offered by urban-rural gradients within human dominated systems, research on tropical urban ecosystems and their constituent components has been scanty (Crane & Kinzig, 2005). In such a context, studies on the organisms which form the apex trophic level in urban ecosystems become extremely important.

Birds exhibit some of the most spectacular spatial displacements to accomplish their daily and periodic activities (e.g. Newton, 2008). Owing to the stringent and acute requirements through these journeys, they have recently become a good model system to study anthropogenic impacts due to shifts in their phenologies and life history parameters (Tryjanowski et al., 2013). Rapid restructuring of urban biological communities (e.g. sympatric competitors, facultative migrant scavengers), and stochastic shifts in the role of *anthropodependent* species (see Hulme-Beaman et al., 2016) are a major concern for rapidly populating cities in the global South (United Nations, 2014). Compared to their rural counterparts, these long and short-term changes modify the behavioural profiles of the individuals interacting with urban ecosystems (Isaksson et al., 2018). Therefore, studies involving commensal birds as model species offer opportunities to investigate the proximate drivers of evolutionarily crafted daily and periodic life history strategies. While research on urban ecology grows exponentially (e.g. Mayer, 2010), most studies have focused on cities of the developed world, which may function in profoundly different ways compared to those of developing countries. In particular, there is a paucity of intensive studies conducted in tropical regions (a severe deficiency highlighted by many reviews, (e.g. Chace & Walsh, 2006; Magle et al., 2012; Marzluff, 2017), despite the fact that rapid urbanization is heavily concentrated in such areas (Grimm et al., 2008; Malakoff et al., 2016).

In the Indian megacity of Delhi, tens of thousands of Black Kites (Milvus migrans, hereafter "kite"), live on the food and other waste made available to kites in intentional and unintentional manners by more than 16 million people. This is probably the largest raptor concentration in the world (Galushin, 1971; Kumar et al., 2014; Naoroji, 2011). By scavenging, and therefore removing waste, kites provide services essential to the health of urban people, both locally and in much of the developing world. Thus, birds such as vultures and kites acquire special significance for people (Ninan, 2009). However, the cultural value of birds in general, and of these commensal birds of prey in particular, extends far beyond the utilitarian. Because south Asian socio-religious diversity, complex interplays of colonization, modernization, urbanization, and technification, have, over four centuries, caused biological extinctions and severed many connections people enjoyed with nature, the disconnection occurring today is unprecedented (Louv, 2006). To address these dynamics, I proposed this interdisciplinary study to document key aspects of cultural knowledge and response to a prominent raptor species in Delhi. Focusing on the experience and traditions of residents of historical Muslim neighbourhoods, I investigated the ecological consequences of these important bird-human relationships. By bringing local perspectives into the available research on urban ecology, I aimed to seed important, two-way relationship of perception: from the side of a facultative scavenger as it adapts to a typical urban life, and the citizens responding to their presence. The quintessential rationale of this research programme was adding quantitative estimates to aid our understanding of the role of human socio-cultural behaviour in shaping urban ecology, by documenting folk-culture and history of valuing diverse ecological knowledges.

The significance of Delhi

Delhi is a megacity of more than 16 million inhabitants, currently covering an area of 1500 km² and in constant, rapid expansion (Census organization of India, 2011). Predicted to be the largest global megacity by 2050 with more than 50 million inhabitants, it is polycentric and heterogeneous, with a multitude of juxtaposed biocultural contexts. One such juxtaposition is the close association of abattoirs and Muslim communities (Sharan, 2014). Urban scavengers such as kites and vultures have historically functioned as vital commensals as they quickly remove meat offal from meat-processing areas. Two aspects of Delhi are important for humanbird interactions (Kumar et al., 2018). First, large areas, usually overlapping with dense human settlements, have poor solid waste management, which affords abundant food such as carrion and organic refuse to animals (e.g., rodents, crows, sparrows, pigeons etc.). Secondly, people (primarily in Muslim communities) engage in a centuries-old practice of feeding meat scraps to kites (so called "ritualized feeding"). These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries (Pinault, 2008). Thus, waste management issues common to all communities, and cultural rituals which are more specific to some, generate spatial heterogeneity in the potential food availability for birds, and constitute a positive feedback loop between ecosystem services and cultural perceptions inducing reverence for these birds. Most importantly, prior quantitative data for this biogeographic region are extremely scarce and previous studies on kites in particular, all of them conducted in the 1970s, have focused on: (1) a coarse estimation of the size of the overall Delhi population (Galushin, 1971), and (2) data on the breeding ecology of a single high-density colony located in the Delhi Zoo (Desai & Malhotra, 1979).

The significance of Black Kites (in context of the recent local collapse of White-backed Vultures)

The Black Kite is a medium-sized opportunistic scavenger, widely distributed throughout Eurasia, Africa and Australia, and considered to be the most successful raptor in the world. Its relationship with humans ranges from active avoidance in Europe to close coexistence with them in Afro-Asia, and the species is synanthropic in India as a city scavenger (Ferguson-Lees & Christie, 2001), occurring in close association with people in towns and cities. Kite distribution and abundance have likely responded to changed spatial distributions of habitat and food sources within Delhi, and may have acquired a portion of the niche previously occupied by vultures prior to their population collapse (see below) in the Indian Subcontinent (Prakash et al., 2003). Kites also contribute by predating rodent pests with consequent benefits for human health (Kumar et al., 2014). In Delhi, kites sometimes form loose colonies, locally reaching extremely high densities thanks to their use of human food 'subsidies' facilitated by inefficient refuse disposal and by religious kite-feeding practices. These large-scale subsidies may explain Delhi's capacity to host what is probably the largest raptor concentration in the world (Kumar et al., 2014).

As this thesis deals with a facultative scavenger species, spending a few words on the recent Indian vulture crisis seems necessary. The Indian sub-continent has been home to nine species of vultures. However, by the year 2000 the region virtually lost its principle avian scavenger, the White-backed Vulture *Gyps bengalensis* (Prakash et al., 2003). The densest livestock population in the world, maintained under poor sanitation around human habitation (Ministry of Agriculture, 2012), allowed vulture populations to thrive in Delhi. Estimated at over 40 million individuals in the country, they primarily occupied all the landfills and carcass

dumping locations of the Delhi capital. Since about 1990, however, vulture numbers have declined by 97% because of carcasses that often contained the veterinary drug Diclofenac, which is fatal for vultures (Prakash et al., 2003). The collapse raised serious issues for waste management and human health, but has also affected the people dependent on its eco-cultural services, e.g. the Parsi community who practiced *dokhmenishini* ("sky burials": see van Dooren, 2010). In urban areas, while the vulture niche has been partially filled by kites and dogs (Markandya et al., 2008), citizens still actively associate the act of scavenging with vultures. Although a ban on Diclofenac and emergency conservation-programmes have been enacted in breeding areas, recovery of the vulture population is still far off. Through this thesis, and under the vision of a long term project in general, I aimed to investigate the ecology of the new main scavenger species of the Delhi urban ecosystem after the vulture collapse. This project also aimed to identify people's perceptions and knowledge of vultures' loss, their response to this population collapse, and acknowledgement of any associative changes in kite numbers at the landfill and in the city in general.

Aims and structure of this thesis

This thesis aimed to investigate the adaptations of a medium-sized raptor to a highly urbanized landscape and the variation of its outcome in terms of breeding success. I dedicated a special focus to the impact of urban structures and waste disposal systems to investigate the relationship between Black Kite density, breeding success and urban planning. The dissertation was planned as a comprehensive assessment of the response of Black Kites to an urban gradient within the megacity of Delhi. The study, currently monitoring the seventh breeding season of resident breeding kite populations in Delhi, is based on a framework of survey-plots that covers most of the observed urbanization gradients, ranging from fully rural to intensively urban settings. Field activities were structured to cover the whole gradient in a continuous manner, i.e. with points scattered all along the gradient rather than through a simplistic dual comparisons between urban vs rural sites. Supplementary material for each data chapter has been provided after the references. Credits for the images, data and figures used in the thesis have been mentioned, unless they are my own. Below, I briefly expose how the thesis has been structured.

1. Chapter 1 introduces and quantitatively describes the natural history and breeding ecology characteristics of the study population of the resident Black Kite subspecies *Milvus migrans govinda*. Here, I report comprehensive quantitative data on density, nest spacing, phenology, breeding success and diet. Subsequently, I compare the current estimates with historical records and with studies on other kite sub-species. This chapter, already published in the journal *Bird Study* (<u>https://doi.org/10.1080/00063657.2013.876972</u>)</u>, is presented in this thesis with an updated sample of 780 nests monitored through the breeding seasons of 2013 - 2018.

2. In Chapter 2, I examined the urban, ecological and human factor that affect nest-site selection along the urbanization gradient, as tested through the comparison of breeding habitat attributes between 154 kite territories and 154 random locations. In addition, I examined the effect of these variables on breeding success and on the rate of territory occupancy, used as an estimate of territory quality. This chapter has already been published in the journal *Urban*

Ecosystems (https://doi.org/10.1007/s11252-017-0716-8)

3. In **Chapter 3**, I focused on a behavioural trait that may mediate kite responses to urbanization, namely the protection of the offspring by parents when "threatened" by humans approaching their nest. This chapter has already been published in the journal *PLoS ONE* (<u>https://doi.org/10.1371/journal.pone.0204549).</u>

4. In **Chapter 4**, I examined the consequences of human-kite interactions, focusing on the peculiar case of aggressive attacks towards humans by kites when defending their nestlings. Here, I modified the analysis of Chapter 3 to compare aggressive pairs that attacked humans with non-aggressive pairs while controlling for the confounding effects of territory quality, season, and previous research-visitation. This chapter is in press in the journal *Scientific Reports* (DOI:10.1038/s41598-019-38662-z).

5. In all previous chapters, the focus has been mainly on individual-level responses to urbanization. In **Chapter 5**, I tested how population-level density responds to urbanization. Here, the large number of plots sampled through the years along the whole urbanization gradient allowed me to apply multivariate models and examine which components of urbanization affect population-level properties. This chapter will build heavily on the analyses of Chapter 2 on individual-level nest-site selection, up-scaling them to the population-level. **This chapter is currently submitted to a high-ranking journal** with a broad ecological audience.

6. Chapter 6 is the last data chapter and is based on GPS-tagging of the migratory *lineatus* subspecies of the Black Kite. Thousands of individuals of this kite subspecies winter within Delhi, in sympatry with the govinda subspecies, which is the main subject of this dissertation. Chapter 6 will be soon submitted to a general ecological journal. Note that during the thesis development, I had occasion to participate to a paper that is directly related to Chapter 6 and which assessed the potential impact of GPS-tagging on Black kites, using data from an intensive tracking-study on a Spanish population. I participated to the statistical analyses of this assessment, as part of my training into radio-tagging, afforded by Dr. F. Sergio and his research group, and aimed at familiarizing myself with radio-tagging techniques and GPS-data processing in order to re-apply these techniques to my Delhi study population. The assessment led to a co-authored paper published in the Journal of Applied Ecology (reference: Sergio, F., Tavecchia, G., Tanferna, A., López Jiménez, L., Blas, J., De Stephanis, R., Marchant, T.A., Kumar, N. & Hiraldo, F. 2015. No effect of satellite tagging on a raptor survival, recruitment, longevity, productivity, social dominance, and its offspring provisioning and condition. Journal of Applied Ecology 52: 1665-1675; https://doi.org/10.1111/1365-2664.12520)

In the **Final Section (Synthesis)**, I recapitulate the findings of all the six data chapters, framing the thesis as the beginning of a long-term study on this species response to urbanization. In particular, I also outline some of the future research themes that I am already developing as part of the ongoing **Phase V (2018- 2020)** of the **Black Kite Project**, funded by the Raptor Research and Conservation Foundation of Mumbai (India) and by the Wildlife Institute of India.

References

- Census Organization of India. (2011). Census of India. Available from: http://censusindia.gov.in/2011census. [Accessed on 25.12.2018].
- Chace, J.F., & Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landscape and Urban Planning* 74: 46-49
- Crane, P., & Kinzig, A. (2005). Nature in the Metropolis. Nature, 5726(1225).
- Desai, J. H., & Malhotra, A. K. (1979). Breeding biology of the pariah kite Milvus migrans at Delhi zoological park. *Ibis*, *121*(3), 320-325.
- Ferguson-Lees, J., & Christie, D. A. (2001). Monk vulture: Aegypius monachus. *Raptors of the World*, 437-438.
- Galushin, V. M. (1971). A huge urban population of birds of prey in Delhi India. *Ibis*, *113*(4), 522-522.
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., & Briggs, J.M. (2008) Global change and ecology of cities. *Science* 319: 756-760
- Hulme-Beaman, A., Dobney, K., Cucchi, T., & Searle, J. B. (2016). An ecological and evolutionary framework for commensalism in anthropogenic environments. *Trends in ecology & evolution*, 31(8), 633-645.
- Isaksson, C., Rodewald, A. D., & Gil, D. (2018). Behavioural and Ecological Consequences of Urban Life in Birds. *Frontiers in Ecology and Evolution*, *6*, 50.
- Kumar, N., Gupta, U., Jhala, Y. V., Qureshi, Q., Gosler, A. G., & Sergio, F. (2018). Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools. *Urban Ecosystems*, 21(2), 339-349.
- Kumar, N., Mohan, D., Jhala, Y. V., Qureshi, Q., & Sergio, F. (2014). Density, laying date, breeding success and diet of Black Kites Milvus migrans govinda in the city of Delhi (India). *Bird study*, 61(1), 1-8.

Louv, R. (2006) Last Child in the Woods. Algonquin Books, N. Carolina.

- Magle, S. B., Hunt, V. M., Vernon, M., & Crooks, K. R. (2012). Urban wildlife research: past, present, and future. *Biological conservation*, *155*, 23-32.
- Malakoff, D., Wigginton, N. S., Fahrenkamp-Uppenbrink, J., & Wible, B. (2016). Rise of the urban planet. *Science*.
- Markandya, A., Taylor, T., Longo, A., Murty, M. N., Murty, S., & Dhavala, K. (2008). Counting the cost of vulture decline—an appraisal of the human health and other benefits of vultures in India. *Ecological economics*, 67(2), 194-204.
- Marzluff, J. M. (2017). A decadal review of urban ornithology and a prospectus for the future. *Ibis*, *159*(1), 1-13.
- Mayer, P. (2010). Urban ecosystems research joins mainstream ecology. *Nature*, 467(7312), 153-154.
- McKinney, M.L. (2010) Urbanization, biodiversity, and conservation. BioScience 52: 883-890
- Naoroji R. (2011). *Birds of prey of the Indian Subcontinent*. Om Books International, ISBN: 978-8-1871-0769-9, 1-692.
- Newton, I. (2008). The migration ecology of birds-Academic Press.
- Ninan, K. N. (2009). Biodiversity ecosystem services and human well-being. *Conserving and Valuing Ecosystem Services and Biodiversity: Economic, Institutional and Social Challenges. Earthscan, London, UK*, 1-22.
- Pickett, S. T., Cadenasso, M. L., Grove, J. M., Nilon, C. H., Pouyat, R. V., Zipperer, W. C., & Costanza, R. (2001). Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Annual review of ecology and systematics*, 32(1), 127-157.
- Pinault, D. (2008) Raw meat skyward: Pariah-kite rituals in Lahore. In: Comparative Islamic studies: notes from the fortune-telling parrot: Islam and the struggle for religious pluralism in Pakistan (Ed. D. Pinault), pp. 108-121, Equinox Publishing Ltd, Bristol, CT, USA.

- Prakash, V., Pain, D. J., Cunningham, A. A., Donald, P. F., Prakash, N., Verma, A., & Rahmani, A. R. (2003). Catastrophic collapse of Indian white-backed Gyps bengalensis and longbilled Gyps indicus vulture populations. *Biological conservation*, 109(3), 381-390.
- Sharan, A. (2014). In the City, Out of Place: Nuisance, Pollution, and Dwelling in Delhi, C. 1850-2000. *OUP Catalogue*.
- Statistics, B. A. H. 19th Livestock census (2012). Department of Animal Husbandry, Dairying and Fisheries, Ministry of Agriculture. Government of India.
- Tryjanowski, P., Sparks, T. H., Kuźniak, S., Czechowski, P., & Jerzak, L. (2013). Bird migration advances more strongly in urban environments. *PLoS One*, *8*(5), e63482.
- United Nations, Department of Economic and Social Affairs, Population Division (2014). *World Urbanization Prospects*: The 2013 Revision, (ST/ESA/SER.A/366)
- van Dooren, T. (2010). Pain of extinction: The death of a vulture. *Cultural Studies Review*, *16*(2), 271-89.

Density, laying date, breeding success and diet of Black Kites *Milvus migrans govinda* in the city of Delhi (India)

Nishant Kumar, Dhananjai Mohan, Yadvendradev V. Jhala, Qamar Qureshi, Fabrizio Sergio Originally published on January 17, 2014; Volume 52, **Bird Study**.

The chapter has been updated with data collected during 2013-2018.

• <u>Published typesetting included in the Appendix</u>

At 16.67 nests/km², the breeding density of Black Kites in Delhi (2013- 2015), India, arguably represents the highest concentration of a medium sized raptor recorded in the world (Galushin, 1971). This study aimed to estimate the density, phenology, breeding success and diet of Black Kites in Delhi through a network of 28 sample plots of 1km² distributed throughout the city. A sample of more than 150 nests was checked regularly to record laying date, breeding success and diet and other nesting ecology parameters. These data were collected to test the hypothesis that Black Kites nesting across these sample plots face marked variation in terms of opportunities and challenges, and this would be reflected in their breeding performance. The surveys done through 2013-2015 found average density estimates to be 16.67 ± 7.9 nests/km². comparable to previous studies values, and ranging from 0 nests/km² to 118 nests/km² across the sampling plots. The majority of nests were on trees and the rest on electric pylons and telephone towers. Mean laying period was late January- early February each year and the laying season was protracted over the five winter-spring months (December - April). The mean number of fledged young was 0.62, 0.89 and 1.33 per territorial (n = 780, from 2013-18), breeding and successful pair respectively. Diet was dominated by scavenged meat and by rats, pigeons and doves abundant in the city. This stability in kite density is probably promoted by a combination of (i) availability of rubbish, (ii) few predators and (iii) high tolerance by people. The conservation status of this raptor seems satisfactory, but removal of mature trees for rapid development may result in local declines or re-distributions, suggesting the need for continued monitoring.

1.1. Introduction

The Black Kite *Milvus migrans* is a medium-sized raptor, currently considered as one of the most numerous and successful birds of prey of the world (Ferguson-Lees & Christie, 2001). It is a generalist, opportunistic feeder, capable of reaching extremely high densities where food concentrations allow it (e.g. review in Malhotra, 2007; Sergio et al., 2005) and may occupy habitats which range from fully natural to completely urban (Ferguson-Lees & Christie, 2001; Ortlieb, 1998). Such adaptability allows it to exploit human-modified habitats, affording the Black Kite, a generally favourable conservation status, with frequent reports of recently increasing populations, despite some local declines (e.g. Bijlsma, 1997; Sergio et al., 2003; Thiollay & Bretagnolle, 2004). This capability to adapt to human landscapes reaches its extreme in populations that nest in fully urban conditions, as frequently observed in Asia and Africa (e.g. Ali & Ripley, 1983; Brown et al., 1982; Desai & Malhotra, 1979; Naoroji, 2006). In these settings, kites are reported not only to use the urban ecosystem for nesting but also for feeding on human offal, road kills, animal carcasses and rubbish, sometimes forming spectacular concentrations of thousands of individuals at rubbish dumps of large cities (Brown et al., 1982; Malhotra, 2007; Naoroji, 2006; Owino et al., 2004). When these dumps are located in the proximity of airports, the concentration of kites often generates serious management problems because of the risk of collisions with planes (e.g. Owino et al., 2004; Satheesan, 1996). It is remarkable that, despite its overall abundance and frequent proximity to humans, Black Kites have very rarely been studied, except for two or three intensively investigated populations, all of them located in Europe and in non-urban settings (e.g. Blanco, 1997; Sergio et al., 2003, 2011; Viñuela et al., 1994).

In the Indian subcontinent, the *govinda* sub-species is well distributed with dense populations in all the major urban centres (Naoroji, 2006). This has attracted many anecdotal observations, as reported in several issues of the Journal of the Bombay Natural History Society (e.g. Abdulali, 1968; Ali, 1926; Fischer, 1906, 1972; Hanxwell, 1892; Mahabal & Bastawade, 1985; Malhotra, 1991). However, quantitative data for this biogeographic region are extremely scarce and previous studies, all of them conducted in the 1970s, have focused on: (1) a coarse estimation of the size of the overall Delhi population (Galushin, 1971) and (2) data on the breeding ecology of the high-density colony of the Delhi Zoo (Desai & Malhotra, 1979). Here, I report comprehensive quantitative data on the density, nest spacing, phenology, breeding success and diet of a fully urban population located within Delhi, India. I then compare the current estimates with historical records and with studies on other kite subspecies.

1.2. Materials and Methods

Study Area

This study builds on work previously undertaken while I was a M.Sc. student at the Wildlife Institute of India, Dehradun. It began at 24 sampling units of 1 km², the area which is regularly monitored each year to document annual variations while each year eight to ten new sampling units are added in the survey scheme. These new plots are monitored only for one year with an aim to have 50-60 plot based uniform coverage for 1500 km² of Delhi by the end of the field work. In each such plot, whose pseudo-replicated number now totals to 79, Black Kites were surveyed through the period 2013 - 2018 (details below, see Appendix). Delhi is a mega-city of 16 million inhabitants in constant, rapid expansion (Census organization of India, 2011). The overall city comprises both urban and semi-urban areas under poor solid waste management, which affords plenty of food to Black Kites in the form of rubbish, carrion and remains from slaughterhouses.

The climate is semi-arid, with a mean annual precipitation of 64 cm, mainly concentrated in July and August. Temperature ranges from a mean maximum of 39.6° C to a minimum of less than 8.2° C in the winter (http://amssdelhi.gov.in/climatology/sfd1.htm). The vegetation of the general region falls within the "northern tropical thorn forest" category (Champion & Seth, 1968).

Field Procedures

Because many areas of the city were private properties not accessible to the public, it was impossible to design a very large continuous study area. Also, because Black Kites in the area can attain extremely high densities, a large number of small plots distributed over a wide area were judged to be better suited to sample all available conditions than a single continuous plot of necessarily limited extension. Therefore, a network of 28 sample plots was designed, each one of approximately 1km², of homogenous accessibility and distributed throughout the city to cover all types of potential nesting habitats. However, a standardized shape or a standardized surface of 1 km² could not be obtained for all plots because of constraints imposed by private properties and logistical difficulties of access. Private properties had similar landscape features to the surrounding areas of the city and I am confident that their exclusion did not bias the density estimates. However, because of the above, nests which were located at the periphery of each sample plot were not employed to generate estimates of nest spacing (nearest neighbour distance, henceforth referred as NND), unless a complete nest census had been conducted also for the area bordering the quadrat.

I surveyed each quadrat repeatedly every few weeks, starting from the pre-incubation period, by walking slowly and carefully inspecting all potential nest structures (trees, buildings, towers etc.). Structures were classified as active nests when a kite individual or pair was repeatedly observed to perch in the nest or its immediate surroundings, or to add material to the nest. Once found, nests were checked by climbing to them, observing them from nearby vantage points, or through an eight-meter telescopic rod equipped with a video-recording camera. Nests were checked approximately every eight days. However, because of time, safety, accessibility and manpower limitations, data on breeding success could not be collected at all nests.

A nest was classified as depredated if I found remains of plucked chicks. Cases of brood reduction (death of one chick, often caused by its siblings, subsequently fed to other nestlings) were not classified as predation events. Hatching date was calculated by backdating from feather development of nestlings first observed when < 15 days old and in comparison with reference information in Desai & Malhotra (1977), Cramp & Simmons (1980), Hiraldo et al. (1990) and personal data by one of the supervisors (FS). Laying date was estimated by subtracting 30 d, the average incubation period (Viñuela, 1997), from hatching date. During each visit, I collected prey remains found inside and under nests and identified them to the genus or species level assuming the smallest possible number of individuals. These items were used to estimate each prey percentage contribution by number or by mass to the diet of Black Kites.

Following Steenhof (1987): a territorial pair was one that built a nest irrespective of whether it then laid a clutch; a breeding or reproductive pair was one which laid eggs; a successful pair was one which raised at least one nestling until it was 40 days old (the chicks fledge when they are 50 days old); and breeding success was the percentage of successful territorial pairs. There was no need to correct the estimates of breeding success through

Mayfield estimators, because all plots were surveyed repeatedly since pre-lay, and because nests were easy to find and were checked very frequently (approximately every eight days). Density was calculated as the number of territorial pairs per unit area and expressed as the number of pairs/km². The difference in breeding success between nests located in trees and nests built on artificial structures was tested by means of a Z-test (Zar, 1984). Throughout, means are given ± 1 SE, tests are two-tailed, and statistical significance was set at $\alpha \le 0.05$.

1.3. Results

Cumulatively, I censused 632 Black Kite nests through 2013 - 2015. Out of these, 595 (94.1%) were located on trees and 37 on artificial structures (electricity pylons and telephone metal towers). Overall, out of the 595 tree nests, 27.9 % were built on Eucalyptus spp., 25.6 % on Ficus spp., 9.8% on Neem (*Azadiracta indica*), 9.2 % on Vilayati Keekar (*Prosopis juliflora*), 9.1 % on Jamun (*Syzygium cumini*) and 18.5% on other tree species such as *Alstonia scholaris*, *Bombax ceiba*, *Dalbergia sisoo* etc (Fig.1.) The mean nest density was 16.67 ± 7.9 pairs/km² and varied between 0 and 118.3 nests / km² (n = 28 plots). Mean nearest neighbour distance for the sampling done in 2013 was 133 ± 15 m and ranged between 5 and 2315 m (n = 207 pairs).



Fig.1. The percent usage of trees and pylons as nesting substrate by the Black Kite population of Delhi (India) in 2013 - 2015 (n = 632).

During 2013-2018, a sample of 780 nests was closely monitored for breeding success. The overall mean laying date was 2nd February (n= 521, SE = 2 days; range 12 December -13 April) and the laying season lasted almost four months each year, with a pronounced peak between the second half of January and first half of February (Fig. 2), a pattern repeated in 2014 and 2015. For a subsample of 151 nests in 2013, when mean monthly temperature and rainfall were superimposed on the laying frequency (Fig. 3), kites seemed to concentrate clutch initiation before the temperatures became excessively high and before the start of the Monsoon rains in June-July. The percentage of clutches initiated each month in 2013 was negatively related to the minimum monthly temperature (linear regression: $B = -1.37 \pm 0.35$; B for constant = 34.21 ± 7.14; n = 12; Bonferroni-corrected P = 0.006; R² = 0.56) and quadratically related to the maximum monthly temperature (quadratic regression: B for linear term = -11.86 ± 3.66 ; Bonferroni-corrected P = 0.02; B for quadratic term: = 0.17 ± 0.06 ; Bonferroni-corrected P =

0.02; B for constant = 211.37 ± 54.04 ; n = 12; R² = 0.77), while egg laying stopped with the commencement of the rains and was initiated again only after the monsoon season. Finally, the number of young fledged by each pair declined with laying date (linear regression: B = - 0.13 ± 0.03 ; B for constant = 1.66 ± 1.77 ; n = 65, P = 0.001; R² = 0.17).



Fig. 2. Temporal frequency of laying dates in the Black Kite population of Delhi (India) in 2013 (n = 65).

Mean clutch size for 2013 - 2018 was 2.13 ± 0.06 (n = 521). Mean hatching success was 84 ± 2.2 % (n = 521 nests). The mean percentage of nestlings lost by brood reduction during 2013-18 was 0.28 ± 4.48 per brood (n = 568 nests). The mean number of fledged young during 2013 -18 was 0.62 per territorial pair (n = 780), 0.89 per breeding pair (n = 521) and 1.33 per successful pair (n = 308). In 2013, forty-eight percent of territorial pairs successfully raised their nestlings to fledging age (n = 151). This value was 55.52 % for 2014 and 39.2% for the 2015

monitoring. Cumulatively, the overall breeding success for a sample of 780 nests (2013- 2018) was 39.49%. For the sampling in 2013, there was a trend for breeding success to be higher for nests on trees than for nest on the artificial structures (46 % vs. 27.8 %; Z = 1.8, P = 0.07, n for tree-nests = 130, n for artificial substrate = 21).

3.1 *Diet*

Kite diet included all vertebrate classes but was strongly dominated, both by mass and number, by three main items: (1) remains from slaughterhouses, mainly in the form of compact chunks of meat; (2) rats; and (3) medium-sized urban birds, such as doves and pigeons (Table 1).

Prey category	Frequency by number (%)	Frequency by mass (%)
Fish ^a	0.8	1.0
Amphibians ^b	0.7	0.7
Reptiles ^c	0.7	0.3
Birds	24.6	31.9
i) Rock Pigeon (Columba livia)	13.1	16.2
ii) Collared Dove (Streptopelia decaocto)	4.1	3.3
iii) Other birds ^d	7.4	12.4
Mammals ^e	9.8	20.2
Scavenged meat ^f	63.4	45.9
i) Meat Scraps	47.1	35.6
ii) Domestic chicken	11.5	6.1
iii) Cattle ^g	4.1	3.5
iv) Fish ^h	0.7	0.7

Table 1. Diet of breeding Black Kites in Delhi, India (2012-13), as estimated by food remains collected inside and under the nest.

^a Includes: unidentified fish (n=1)

^b Includes: Indian bullfrog (n = 1).

^c Includes: Common house gecko (n = 1).

^d Includes: Moorhen (Gallinula chloropus) (n=1), Indian Roller (Coracias benghalensis) (n=1),

Unidentified birds (n=7)

^e Mammals which were unlikely to be consumed as carrion. Includes: Norway rat (*Rattus norvegicus*) (n = 11) and Palm squirrel (*Funambulus pennantii*) (n = 1)

^f Includes prey items that were considered to have been collected as carrion from local rubbish dumps and slaughterhouses.

^g Includes: Buffalo (n=2), Goat (n=3).

^h Includes: Large unidentified fish skin, likely from fish market.

1.4. Discussion

The study confirms that Black Kites have maintained extremely high breeding densities throughout the city of Delhi, as already observed in the 1970s (Galushin, 1971). When compared with data from other populations (reviewed in Table 2), the density observed in the urban environment of Delhi was higher than any previously published estimate. This is then, probably, the highest density ever recorded over a large, continuous area for any bird of prey of this size. The capability to attain such a high population-level over such a large region is likely to be promoted by a combination of at least three factors. (1) First, the rubbish management plans of such a rapidly developing mega-city are inevitably poor, which results in a network of enormous, legally-authorized rubbish dumps coupled with hundreds of smaller, and often illegal sites where garbage is dumped daily. At an even finer-scale, private individuals, families and shops often leave their daily garbage directly in the streets, resulting in a network of ephemeral, small piles of food. In turn, these must promote large populations of potential prey species, such as rats and pigeons. All the above, coupled with the high abundance of meat and fish shops throughout the city, sets an ideal scenario of enormous food availability for an opportunistic predator and facultative scavenger. (2) Second, the attitudes of local people towards kites, and wildlife in general, are extremely positive and tolerant, even despite the fact that some kites can be very aggressive in defending their nest against nearby passers-by. I am not aware of any cases of persecution of kites in Delhi, which is confirmed by the relative absence of fear of humans shown by most kites in comparison to European conspecifics. (3) Third, the city provides an environment with a low abundance of potential predators. The only potential nest predators known to occur locally are Indian Eagle Owls Bubo bubo bengalensis, House Crows Corvus splendens and Rhesus Macaques Macaca mulatta. The latter two species can be locally

abundant, but are often deterred by the very aggressive and effective nest defence behaviour of parent kites.

When compared to historical records, the high density record seemed remarkably stable over several decades. However, rapid city-wide surveys and data from the New Delhi Zoological Park suggested much higher current densities than had been observed previously (Desai & Malhotra, 1979; Galushin, 1971; see Table 2). This likely resulted from the enormous changes in the city's dimensions, population size and management, although, the overall density of the NZP area (3 km² area which included 40 acre of NZP) remained stable. In a way, the differential sectoral development in the city tends to do both, support or reduce kite density, depending upon local development and juxtaposition of favourable habitat patches and food resources. Such positive overall status is in place despite the recent, virtual extinction of the locally abundant populations of a potential trophic competitor, the White-rumped Vulture *Gyps bengalensis*, the former primary scavenger (Naoroji, 2006; Prakash et al., 2003). The kite population thus seemed very resilient to change in terms of overall density.

Table 2. Breeding density and nest spacing of Black Kite populations in Europe and India (Delhi), 1966-2015. Density was expressed as territorial pairs/ 10 km^2 for clarity of presentation. The 2013 - 15 data from the current study are presented twice in the table: (i) for the whole study area, i.e. representative of the whole Delhi population; and (b) for the high-density sector of the New Delhi National Zoological Park (NZP), in order to make them comparable to historical data from the 1970s by Malhotra (2007).

Area (period)	Habitat	Density (per/10 km ²) (n)	Nearest neighbour distance in meters (n)
Delhi, India (2015) ¹⁷	U	170 (231)	-
NZP, India (2015) ¹⁷	U	1093 (70)	-
Delhi, India (2014) ¹⁷	U	183 (157)	
NZP, India (2014) ¹⁷	U	1183 (71)	-
Delhi, India (2013) ¹⁷ Delhi, India (1967-1969) ³	U U	150 (244) 161 (~560)	133 (207)
NZP, India (1979) ¹⁶	U	250 (18-21)	-
NZP, India (2013) ¹⁷	U	870 (70)	-
Matas Gordas, Spain (1987-1989) ¹⁰	М	70-150 (21-45)	-
Matas Gordas, Spain (1992-2000) ¹⁵	М	100.8 (515)	-
Doñana, Spain (1981-1984) ⁸	М	26.7 (80)	206 (47) ^a
RBD, Spain (1989–2000) ¹⁵	М	15.1 (1059)	-
Lac Leman, Switzerland (1975-1990) ¹¹	F	10.1 (319)	-
Neuchatel, Switzerland (1968) ⁵	FL	7.1 (337)	-
Lorraine, France (1966) ¹	WP	4.5 (66)	-
Rhône Plain, France (1970) ⁵	RP	60.9 (140)	-
Limousin, France (1976-1978) ⁴	PW	1.0 (21)	-
Lake Lugano, Italy (1992-1996) ¹³	WL	2.4-3.8 (27-41)	441 (175)
Lake Lugano, Italy (1992–2003) ¹⁵	WL	2.9 (365)	-
Lake Maggiore, Italy (1996–2000) ¹⁴	WL	- (24)	-
Lake Como, Italy (1996–2000) ¹⁴	WL	4.7 (40)	-
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Lake Iseo, Italy (1996–2000) ¹⁴	WL	3.5 (48)	-
Lake Idro, Italy (1997–2001) ¹⁴	WL	6.7 (37)	-
Lake Garda, Italy (1997–2000) ¹⁴	WL	1.5 (18)	-
Sarca Valley, Italy (1997–2003) ¹⁴	WL	1.3 (88)	-
Castelporziano, Italy (1991-1992)9	WF	3.3 (16)	103 (16) ^b
Monti della Tolfa, Italy (1973-1980) ⁷	WP	0.5 (42)	-
Costance Lake, Germany (1968-1969) ²	FL	1.9-2.2 (25-30)	-
Drömling, Germany (1993-1994) ¹²	F	0.7 (8)	2330 (8) °
Brandenburg, Germany (1979) ⁶	F	0.7 (215)	-

^a Estimate from Bustamante & Hiraldo (1990), for the period 1985-1988.

^b Refers to a single colony.

^c Calculated from the published map.

U: Urban, M: Marshland, FL: Farmland & Lake, WL: Woodland & Lake, F: Farmland, WP:

Woodland & Pasture, WF: Woodland & Farmland , FL: Farmland & Lake, PW: Pasture & Woodland, RP: River Plain

¹Thiollay 1967, ²Heckenroth 1970, ³Galushin 1971, ⁴Nore 1979, ⁵Sermet 1980, ⁶Fiuczynski 1981,

⁷Petretti & Petretti 1981, ⁸Hiraldo et al. 1990, ⁹De Giacomo et al. 1993, ¹⁰Viñuela et al. 1994,

¹¹Henrioux & Henrioux 1995, ¹²Seelig *et al.* 1996, ¹³Sergio & Boto 1999, ¹⁴Sergio *et al.* 2003, ¹⁵Sergio *et al.* 2005, ¹⁶Malhotra 2007, ¹⁷This study

The laying season was protracted over almost four months, probably as a result of the long period of warm, favourable weather and of the stable food supply provided by the urban environment (Fig. 3). The temporal peak and range of laying dates seemed to be arranged so that most nestlings fledged well before the high temperatures and the marked peak in precipitation caused by Monsoon rains in July-August (Fig. 3). The negative effect of high temperatures and rainfall on kite foraging performance, egg viability and breeding success has been reported for various European populations (Hiraldo et al., 1990; Sergio, 2003; Viñuela, 2000). The observed, lengthy range of laying dates compares to a duration of the laying season of 28 days for kite populations of the Italian Alps and to 2.8 months for the population of Doñana

National Park, in the extreme south of Europe (F. Sergio, pers. data). This suggests a North-South latitudinal gradient in the length of kite breeding seasons. Protracted breeding seasons are increasingly reported as progressively more studies of birds of prey are conducted in tropical or more southern latitudes (e.g. Ogada & Kibuthu, 2012; Simmons, 2000).



Fig.3. Mean temperature, monthly rainfall and Black Kite laying frequency in 2013 in Delhi (data from: <u>http://amssdelhi.gov.in/climatology/sfd1.htm</u>).

When compared to other populations (review in Table 3), my estimates of breeding success were lower than in other studies and this may be a consequence of density-dependent processes in a crowded, saturated population (e.g. Newton, 1998). The fact that similarly low levels of reproduction were reported for another saturated population (Doñana, Sergio et al., 2011) lends support to this impression (Fig. 4). However, in the absence of more information, other alternative explanations cannot be discounted: for example, it is not known whether a diet based

largely on rubbish and meat produced for human consumption could spread pathogens or toxic substances among the offspring. In addition to this, I observed considerable loss of chicks during the 2015 season to avian pox, a disease which only affects the nest bound offsprings. Nine out of 10 nests, with fledglings having cases of avian pox (late April 2015) in NZP, suffered eventual failure. This was likely caused by the heavy and abrupt downpour in March 2015 which increased the population of insect vectors of the disease (Unpublished, camera trap data).



Fig.4. The relationship between the nest density of Black Kite populations in Asia and Europe, and the **mean breeding success** over several years.

Table 3 Productivity of Black kite populations in Europe and Asia, 1966-2015. The 2013 -18 data from the current study are presented twice in the table: (i) for the whole study area, i.e. representative of the whole Delhi population; and (ii) for the high-density sector of the New Delhi National Zoological Park (NZP), in order to make them comparable to historical data from the 1970s by Desai & Malhotra (1979).

Area (period)	Habitat (n)	Clutch size	Hatching success ^a (eggs)	Breeding success	Mean number of fledged young		
					territorial pair	breeding pair	successful pair
Delhi, India (2013-2018) ¹¹	U (780)	2.13(521) ^b	84% (521) ^b	39.49%	0.62	0.89(521) ^b	1.33 (308) ^b
Delhi, India (2015) ¹¹	U (212)	2.14 (193)	65.9 % (106) ^b	39.2%	-	5	-
Delhi, India (2014) ¹¹	U (157)	-	-	55.5%	-	-	-
Delhi, India (2013) ¹¹	U (151)	2.09(100) ^b	68% (157) ^b	48%	0.73	1.09(100) ^b	1.52 (72) ^b
NZP, India (1973-1976) ²	U (45)	2.3 (60) ^b	55% (102) ^b	-	0.98	-	-
NZP Park, India (2013) ¹¹	U(46)	2.04 (36)	62% (55) ^b	59%	0.78	0.95 (38) ^b	1.44 (25) ^b
RBD,Spain (1989–2000) ¹⁰	WL(1059)	2.02	67.4 % (416)	41%	0.59	0.71	1.43
Matas Gordas, Spain (1992–2000) ¹⁰	GM(515)	2.12	70.3 % (232)	44%	0.61	0.85	1.46
Germany (1992-1995)7c	-(599)	-	-	79%	1.63	-	2.07 (471) ^b
Limousin, France (1976-1978) ³	PW (22)	-	9 8	68%	-	1.32	1.93 (15) ^b
Berlin, Germany (1940-1979) ⁴	F (215)	93 <u>8</u> 4	<u> </u>	62%	1.20		1.90 (133) ^b
Lake Lugano, Italy (1992-1996)9	WL (143)	2.29 (42) ^b	84% (96) ^b	55%	0.97	1.1 (95) ^b	1.78 (78) ^b
Lake Lugano, Italy (1992-2003)10	WL (315)	2.3	74 % (88)	50%	0.90	1.24	1.80

WL (30)			50%	0.87	-	1.73
WL (40)	-		48%	0.75	1570	1.58
WL (48)	-		38%	0.48	-	1.10
WL (37)	1.31	10 75	59%	1.05		1.63
WL (18)	-	-	44%	0.83	-	2.14
WL (88)	-	12	40%	0.63	-	1.62
- (162)	2.98 (44) ^b	-	×		2.31	-
FL (165)	2.25	а <u>н</u>	-	-	2.02	-
WP (66)	2.26 (45) ^b	-	5	1.32	1.58 (55) ^b	-
FP (32)	2.18 (28) ^b	79% (61) ^b	75%	1.00	1.14 (28) ^b	1.33 (24) ^b
	WL (30) WL (40) WL (48) WL (37) WL (18) WL (88) - (162) FL (165) WP (66) FP (32)	 WL (30) - WL (40) - WL (48) - WL (37) - WL (18) - WL (88) - - (162) 2.98 (44)^b FL (165) 2.25 WP (66) 2.26 (45)^b FP (32) 2.18 (28)^b 	WL (30) - - WL (40) - - WL (48) - - WL (37) - - WL (18) - - WL (88) - - - (162) 2.98 (44) ^b - FL (165) 2.25 - WP (66) 2.26 (45) ^b - FP (32) 2.18 (28) ^b 79% (61) ^b	WL (30)50%WL (40)48%WL (48)38%WL (37)59%WL (18)44%WL (88)40%- (162)2.98 (44) bFL (165)2.25WP (66)2.26 (45) bFP (32)2.18 (28) b79% (61) b75%	WL (30)50%0.87WL (40)48%0.75WL (48)38%0.48WL (37)59%1.05WL (18)44%0.83WL (88)40%0.63- (162)2.98 (44) bFL (165)2.25WP (66)2.26 (45) b1.32FP (32)2.18 (28) b79% (61) b75%1.00	WL (30)50% 0.87 -WL (40)48% 0.75 -WL (48)38% 0.48 -WL (37)59% 1.05 -WL (18)44% 0.83 -WL (88)40% 0.63 (162) 2.98 (44) b2.31FL (165) 2.25 2.02WP (66) 2.26 (45) b 1.32 1.58 (55) bFP (32) 2.18 (28) b 79% (61) b 75% 1.00 1.14 (28) b

^a Data on hatching success not shown in table: 75% (N = 36 eggs from 14 nests, Hakel, Germany, 1957; Stubbe 1961) and 64% (N = 28 eggs from 10 nests, Lazio, Italy, date unknown; Petretti 1992).

^b Sample size (when different from that in column "Habitat (n)").

^c Data also from Mammen & Stubbe (1995, 1996)

U: Urban, GM: Grassland & Marshland, FL: Farmland & Lake, WL: Woodland & Lake, F: Farmland, WP: Woodland & Pasture, FL: Farmland & Lake, PW: Pasture & Woodland, FP: Fishing Port

¹Thiollay 1967, ²Desai & Malhotra 1979, ³Nore 1979, ⁴Fiuczynski 1981, ⁵Danko 1989, ⁶Koga et al. 1989, ⁷Gedeon 1994^e, ⁸Henrioux & Henrioux 1995, ⁹Sergio & Boto 1999, ¹⁰Sergio et al. 2005, ¹¹This study

Finally, the observed diet composition confirmed the full dependence of the local kite population on urban resources, such as meat scraps from slaughterhouses or prey species which were extremely abundant within the city, such as rats, feral pigeons and wild dove species. The current picture of the diet does not suggest that kites range frequently, if at all, out of the city to capture wild prey in surrounding rural areas. This confirms that the high density attained within the urban setting is promoted by attraction to a dense food source. Regarding the estimates of various prey components of the breeding kites' diet (Table 1), it must be noted that representation of boneless meat chunks are unlikely to be justified by opportunistic sampling of prey remains. Therefore, our estimates must be treated as cursory, with scope of improvement by deployment of trail cameras which can monitor nest activities 24 x 7 (see Chapter 5). Use if cameras would address the likelihood of bias in context of meat chunks, which did not leave any remains for us to factor in the diet analyses.

In summary, extensive foraging opportunities, a stable favourable climate, absence of human persecution and low density of potential predators have probably contributed to one of the densest raptor populations of the world. The current conservation status of the studied population seems satisfactory, but recent urban development is causing extreme and almost complete removal of mature trees in some sectors of the city. In turn, this could limit the kite population in the future, or trigger local declines and re-distributions, especially when considering that artificial structures do not seem to fully compensate for the absence of trees (Fig. 1, Chapter 5). Thus, given the abundance of the species and the current urban sanitary levels, the ecological service provided by kites through removal of organic rubbish must be valuable, suggesting the need for ecologically sensitive urban planning of the remaining green

areas. This calls for the importance of continued monitoring of the population and its nesting requirements in future years.

References

- Abdulali, H., & Nair, J. G. (1968). Extension of the range of the large Indian Kite Milvus migrans lineatus (Gray). *J. Bombay Nat. History Soc*, 65, 774.
- Abdulali, H. (1972). Some bird notes by WF Sinclair. J. Bombay Nat. History Soc, 69, 422-424.
- Ali, S., & Ripley, D.A. (1983). No. 132. Black Kite (*Milvus migrans migrans*) (Boddaert), *Handbook of the Birds of India and Pakistan*. Oxford University Press, New Delhi, Volume 1 (Divers to Hawks) 226.
- Ali, S. (1926). Mating habits of common Pariah Kite (Milvus migrans govinda). J. Bombay Natl. Hist. Soc, 31, 524-526.
- Baccetti, N. (Eds.) (1992). Fauna d'Italia . Edizioni Calderini, Bologna, italy.
- Bijlsma, R.G. (1997). Black Kite. In The EBCC Atlas of European breeding birds, their distribution and abundance, eds. W.J.M. Hagemeijer, & M.J. Blair, M. J, 132-133. T & AD Poyser, London.
- Blanco, G. (1997). Role of refuse as food for migrant, floater and breeding Black Kites (Milvus migrans). *Journal of Raptor Research*, 31, 71-76.
- Brown, L. H., Urban, E. K., & Newman, K. (1982). The Birds of Africa, Vol. 1. London. Academic Press, London.
- Bustamante, J., & Hiraldo, F. (1990). Adoptions of fledglings by black and red kites. *Animal behaviour*, *39*, 804-806.
- Census Organization of India. (2011). Census of India. Available from: http://censusindia.gov.in/2011census [accessed 27 September 2015]
- Champion, S. H., & Seth, S. K. (1968). A revised survey of the forest types of India. *Manager* of *Publications*, Government of India, New Delhi.
- Cramp, S., & Simmons, K. E. L. (1980). *Handbook of the birds of Europe, the Middle East and North Africa*. Vol. 2. Hawks and bustards. Oxford Univ. Press, Oxford, U.K.

Danko, Š. (1989). Five young in the nest of a Black Kite (Milvus migrans). Buteo. 4, 87-92.

- De Giacomo, U., Martucci, O., & Tinelli, A. (1993). L'alimentazione del Nibbio bruno (Milvus migrans) nella Tenuta di Castelporziano (Roma). *Avocetta*, *17*, 73-78.
- Desai, J. H., & Malhotra, A. K. (1979). Breeding biology of the pariah kite Milvus migrans at Delhi zoological park. *Ibis*, *121*(3), 320-325.
- Ferguson-Lees, J., & Christie, D. A. (2001). Monk vulture: Aegypius monachus. *Raptors of the World*, 437-438.
- Fischer, C. E. C. (1906). Flocking of Kites. Journal of the Bombay Natural History Society. 17(2), 525 - 526.
- Fiuczynski, D. (1981). Berliner milan-chronik (Milvus migrans and Milvus milvus). Beitr. Vogelk, 27, 161-196.
- Galushin, V. M. (1971). A huge urban population of birds of prey in Delhi India. *Ibis*, *113*(4), 522-522.
- Gedeon, K. (1994). Monitoring Greifvögel und Eulen: Grundlagen und Möglichkeiten einer langfristigen Überwachung von Bestandsgrö [beta] en und Reproduktionsdaten. Martin-Luther-Universität.
- Hanxwell, T. A. (1892). Nest and eggs of the Crested Black Kite. *Journal of the Bombay Natural History Society*, 7(3), 403-404.
- Heckenroth, H. (1970). Der Greifvogelbestand des Bodanrücks (Bodensee) 968 und 1969. *Anz. Orn. Ges. Bayern*, 9, 47-51.
- Hiraldo, F., Veiga, J. P., & Mañez, M. (1990). Growth of nestling black kites Milvus migrans: effects of hatching order, weather and season. *Journal of Zoology*, *222*(2), 197-214.
- Indian Meteorological Department. (2013). <u>http://amssdelhi.gov.in/climatology/sfd1.htm</u>. [Accessed 27 September 2015].

- Koga, K., Siraishi, S., & UCHIDA, T. (1989). Breeding ecology of the Black-eared Kite Milvus migrans lineatus in the Nagasaki Peninsula, Kyushu. *Japanese Journal of Ornithology*, 38(2), 57-66.
- Mahabal, A., & Bastawade, D. B. (1985). Population ecology and communal roosting behaviour of pariah kite Milvus migrans govinda in Pune (Maharashtra). *Journal of the Bombay Natural History Society. Bombay*, 82(2), 337-346.
- Malhotra, A.K., (1991). Site fidelity and power of recognition in Pariah Kite *Milvus migrans* govinda, Journal of the Bombay Natural History Society, 87, 458.
- Malhotra, A.K. (2007). Tiger of sky-Pariah Kite, PhD thesis, Shilalekh Publishers, Delhi.
- Mammen, U., & Stubbe, M. (1996). Jahresbericht 1995 zum Monitoring Greifvögel und Eulen Europas. *Jahresbericht zum Monitoring Greifvögel und Eulen Europas*, 8.
- Mammen, U., & Stubbe, V. (1995). Jahresbericht 1994 zum monitoring Greifvögeln und Eulen Europas Jahresber. *Monitoring Greifvögel Eulen Europas*, 7(1),78.
- Naoroji, R. (2006). Birds of prey of the Indian subcontinent. Christopher Helm.
- Newton, I. (1998). Population limitation in birds. Academic press.
- Nore, T. (1979). Rapaces diurnes communs en Limousin pendant la periode de nidification (Buse, Bondre, Milan noir, Busards saint-martin et Cendre). *Alauda*. 47,183-194.
- Ogada, D. L., & Kibuthu, P. M. (2012). Breeding ecology of Mackinder's Eagle-Owls (Bubo capensis mackinderi) in farmlands of central Kenya. *Journal of Raptor Research*, *46*(4), 327-335.
- Ortlieb, R. (1998). Der Schwarzmilan. Die Neue Brehm-Bücherei, Hohenwarsleben, Germany
- Owino, A., Biwott, N., & Amutete, G. (2004). Bird strike incidents involving Kenya Airways flights at three Kenyan airports, 1991–2001. *African Journal of Ecology*, *42*(2), 122-128.
- Peteretti, F. (1992). Nibbio bruno. 459-465 in P. Brichetti, P. De Franceschi & N.

- Petretti, A., & Petretti, F. (1981). A population of diurnal raptors in central Italy. *Gerfaut*, 71, 143-156.
- Prakash, V., Pain, D. J., Cunningham, A. A., Donald, P. F., Prakash, N., Verma, A., & Rahmani,
 A. R. (2003). Catastrophic collapse of Indian white-backed Gyps bengalensis and longbilled Gyps indicus vulture populations. *Biological conservation*, 109(3), 381-390.
- Satheesan, S.M. (1996). Raptors associated with Airports and Aircrafts; *Raptors in Human landscapes*. Academic press limited.
- Seelig, K. J. (1996). Die Vögel im Naturpark Drömling. Förderkreis Museum Heineanum.
- Sergio, F., Blas, J., Forero, M., Fernández, N., Donázar, J. A., & Hiraldo, F. (2005). Preservation of wide-ranging top predators by site-protection: black and red kites in Doñana National Park. *Biological Conservation*, 125(1), 11-21.
- Sergio, F., Blas, J., López, L., Tanferna, A., Díaz-Delgado, R., Donázar, J. A., & Hiraldo, F. (2011). Coping with uncertainty: breeding adjustments to an unpredictable environment in an opportunistic raptor. *Oecologia*, 166(1), 79-90.
- Sergio, F., Pedrini, P., & Marchesi, L. (2003). Reconciling the dichotomy between single species and ecosystem conservation: black kites (Milvus migrans) and eutrophication in pre-Alpine lakes. *Biological Conservation*, 110(1), 101-111.
- Sergio, F. (2003). From individual behaviour to population pattern: weather-dependent foraging and breeding performance in black kites. *Animal Behaviour*, *66*(6), 1109-1117.
- Sergio, F., & Boto, A. (1999). Nest dispersion, diet, and breeding success of Black Kites (Milvus migrans) in the Italian pre-Alps. *Journal of Raptor Research*, *33*, 207-217.
- Sermet, E. 1980. *Milan noir*. Pages 88-89 in Schifferli, A. (1980). *Atlas des oiseaux nicheurs de Suisse*. Schweizerische Vogelwarte Sempach.
- Simmons, R. E., & Simmons, J. R. (2000). *Harriers of the world: their behaviour and ecology* (Vol. 11). Oxford University Press on Demand.

- Steenhof, K. (1987). Assessing raptor reproductive success and productivity. *Raptor management techniques manual*, 157-170.
- Stubbe, C. (1961). Die Besiedlungsdichte eines abgeschlossenen Waldgebietes (Hakel) mit Greifvögeln im Jahre 1957. *Beitr. Vogelkd*, 7, 155-224.
- Thiollay, J.M., & Bretagnolle, V. (2004). Rapaches nicheurs de France: distribution, effectifs et conservation. *Delachaux et Niestlé*, Paris, France.
- Thiollay, J. M. (1967). Ecologie d'une population de rapaces diurnes en Lorraine.
- Viñuela, J., Villafuerte, R., & Court, C. D. L. (1994). Nesting dispersion of a black kite population in relation to location of rabbit warrens. *Canadian Journal of Zoology*, 72(9), 1680-1683.
- Viñuela, J. (1997). Laying order affects incubation duration in the Black Kite (Milvus migrans): Counteracting hatching asynchrony? *The Auk*, 192-199.
- Viñuela, J. (2000). Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. *Behav. Ecol. Sociobiol, 45*, 333-343.
- Zar, J. H. (1984). Bio-statistical analysis. Englewood Cliffs, NJ: Prentice-Hall, 283.



Appendix: Delhi Master plan map 2021 (source: Municipal Corporation of Delhi), with the sampling units (the larger bi-colour dots depict the sampling units followed each year to monitor annual variations, while the single colour dots represent the sampling units followed only once).

Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as preyfacilitating tools

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Originally published on December 18, 2017; Volume 51(2), Urban Ecosystems.

- <image>
- Published typesetting included in the Appendix

Abstract

Research in urban ecology is growing rapidly in response to the exponential growth of the urban environment. However, few studies have focused on tropical megacities, and on the interplay between predators' habitat selection and human socio-economic aspects, which may mediate their resilience and coexistence with humans. We examined mechanisms of breeding habitat selection by a synanthropic raptor, the Black Kite Milvus migrans, in Delhi (India) where they mainly subsist on: (1) human refuse and its associated prey-fauna, and (2) ritualised feeding of kites, particularly practiced by Muslims. We used mixed effects models to test the effect of urban habitat configuration and human practices on habitat selection, site occupancy and breeding success. Kite habitat decisions, territory occupancy and breeding success were tightly enmeshed with human activities: kites preferred areas with high human density, poor waste management and a road configuration that facilitated better access to resources provided by humans, in particular to Muslim colonies that provided ritual subsidies. Furthermore, kites bred at 'clean' sites with less human refuse only when close to Muslim colonies, suggesting that the proximity to ritual-feeding sites modulated the suitability of other habitats. Rather than a nuisance to avoid, as previously portrayed, humans were a keenly-targeted foraging resource, which tied a predator's distribution to human activities, politics, history, socio-economics and urban planning at multiple spatio-temporal scales. Many synurbic species may exploit humans in more subtle and direct ways than was previously assumed, but uncovering them will require greater integration of human socio-cultural estimates in urban ecological research.

Keywords: Urban ecology; Food subsidies; Muslim; Ritual feeding; Synurbic; Urbanization



A view from a Black Kite nest on a pylon in Delhi, depicting the selection pressures offered by steep habitat edges (Chapter 2 and 5).

2.1. Introduction

Urban ecosystems are spreading rapidly, with more than 50 % of the global human population currently concentrated in cities, a figure estimated to reach 66 % by 2050 (United Nations, 2014). Ninety-eight percent of this net increase is expected to happen in cities in developing countries (Grimm et al., 2008), so that by the middle of the 21st century 75 % of urban dwellers will be located in Asia and Africa (Anonymous, 2016). Such urban sprawl has welldemonstrated ecological consequences, including disruption of energy flow and nutrient cycles, habitat degradation, increased carbon emissions, and the extinction of many species (e.g. McKinney, 2010; Pickett et al., 2001). Nevertheless, some animal species have managed to adapt and thrive under such conditions (Lepczyk et al., 2017). Some, for example, can take advantage of human waste and reach densities that are not otherwise encountered (Brook et al., 2003; Gangoso et al., 2013; Inger et al., 2016). These urban exploiters are often alien invaders seen as 'nuisances to eradicate' (e.g. Belant, 1997; Brook et al., 2003; Kurosawa et al., 2003), but can also be native species that have co-existed with humans for millennia, and so are preadapted to urban conditions and appreciated for their cultural significance (reviews in Hosey & Melfi, 2014; Soulsbury & White, 2015). Studying these synanthropic species is important for several reasons. First, they offer unique insight into the capacity of animals to withstand and even exploit human activity, thus adapting to a growingly urban world. Second, their abundance and frequent commensalism with humans makes them an integral part of the human cultural landscape, potentially making them important components of people's sense of connection with nature (e.g. Cox & Gaston, 2016; Fuller et al., 2012; Nilon, 2011). Third, many of them are facultative scavengers that subsist on animal carrion and human waste, thus providing fundamental ecosystem and sanitary services, as well demonstrated in urban and rural

environments (e.g. Gangoso et al., 2013; Inger et al. 2016; Margalida & Colomer, 2012; Moleón et al., 2014). Fourth, they are often dominant components of the community, potentially limiting other species, and thus contributing to faunal homogenization (Carey et al., 2012; McKinney, 2006; Shochat et al., 2010). Finally, these species could indicate the future behavioural and demographic characteristics of exotic urban invaders when they reach a mature stage of colonization. However, despite all the above, relatively few intensive studies have centred on these 'synanthropic' urban exploiters (e.g. Marzluff et al., 2001; Parker & Nilon, 2012).

While research on urban ecology grows exponentially (e.g. Mayer, 2010), several areas have received limited attention. In particular, there is a paucity of intensive studies conducted in tropical regions (a severe deficiency highlighted by many reviews, e.g. Chace & Walsh, 2006; Magle et al., 2012; Marzluff, 2016), despite the fact that urbanization will be heavily concentrated in such areas over the coming decades (Malakoff et al., 2016). Scarce research attention has also been devoted to megacities (cities with > 10 million inhabitants), most of which are themselves concentrated in developing tropical countries (Grimm et al., 2008; Malakoff et al., 2016). Furthermore, few studies have focused on facultative scavengers or top predatory species, probably because much of the urban fauna is dominated by small species with diets dominated by plant material (e.g. Evans et al., 2011). Finally, despite the obvious significance of humans to the very existence of the urban environment, remarkably few authors have either incorporated human socio-economic factors as an integral component of their ecological research (e.g. Grimm et al., 2000; Liu et al., 2007), or focused on habitat selection by individual animals, which may yield important insight into mechanisms of resilience enabling close coexistence with humans.

To contribute to these overlooked areas, we examined habitat selection by a synanthropic native top predator in the tropical megacity of Delhi, India, currently the second most populous city in the world. Here, we demonstrate that its habitat choices are tightly intertwined with human activities, including specific socio-religious practices, which greatly influence the spatial distribution of food subsidies.

2.2. Materials and Methods

Model species

The Black Kite *Milvus migrans* (hereafter kite) is a medium-sized opportunistic raptor, widely distributed throughout Eurasia, Africa and Australia, and considered as the most successful raptor in the world. In India, the native, resident subspecies *M. m. govinda* is synurbic (Francis & Chadwick, 2012), i.e. occurring almost exclusively in close association with humans in towns and cities (Naoroji, 2006). In Delhi, kites breed on both trees and artificial structures (pylons, towers), sometimes forming loose colonies and locally reaching extremely high densities, thanks to the exploitation of human food subsidies facilitated by inefficient refuse disposal and by religious kite-feeding practices (Kumar et al., 2014; see details below). These large-scale subsidies may explain Delhi's capacity to host what is probably the largest raptor concentration in the world (Galushin, 1971; Kumar et al., 2014).

Study Area

Delhi is a megacity of more than 16 million inhabitants, currently covering an area of 1500 km² and in constant, rapid expansion (<u>http://censusindia.gov.in/2011census</u>). It is polycentric and heterogeneous, with a multitude of urban configurations, which make it difficult to establish a linear urban-rural gradient. The climate is semi-arid, with a mean annual precipitation of 640

mm, mainly concentrated in July and August during the monsoon season. Temperature ranges from a minimum mean value of 8.2°C in the winter to a maximum mean value of 39.6°C during the summer (see <u>http://amssdelhi.gov.in/climatology/sfd1.htm</u>). The vegetation of the general region falls within the 'northern tropical thorn forest' category (Champion & Seth, 1968).

Two aspects of Delhi are important for kite foraging. First, large portions of the city are characterized by poor solid waste management, which affords plenty of food to kites in the form of carrion or refuse, and its associated prey-fauna (e.g. rodents, pigeons etc.). Second, many people engage in the centuries-old religious practice of feeding meat scraps to kites (hereafter termed "ritualized-feeding") typically offered by throwing meat into the air for the birds to catch. These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries (Pinault, 2008; Taneja, 2015). Whilst meat-offering is practiced by a number of communities, in Delhi, it is especially prevalent amongst members of the Muslim faith, whose numbers are concentrated in well-defined portions of the city (hereafter "Muslim colonies"). In these areas, ritualized-feeding is operated both by private individuals, and as public events, typically around mosques, where large quantities of meat are tossed to kites at predictable hours each day, sometimes causing hundreds of kites to congregate. Thus, waste management issues common to all communities, and cultural rituals which are more specific to some, generate spatial heterogeneity in the potential food availability for kites.

Field procedures

We surveyed kite nests systematically over the four years 2013–2016 at 24 plots of 1 km². These were plotted strategically within Delhi (1500 km²) so as to cover all its possible urban settings, from semi-natural to extremely built-up sites (details in Kumar et al., 2014). This resulted in a

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sample of 154 nests, each from a different territory, used at least once for breeding between 2013 and 2016. Nests were checked every 7-10 days until the chicks were at least 45 days old, in order to estimate the number of young raised to fledging (chicks fledge when about 48 days old; see Kumar et al., 2014 for further details of nest checks and surveys).

Breeding site characteristics

To investigate nest-site selection, we compared the urban, human and environmental variables collected at the 154 nests (see below) with those collected at an equal number of random locations, generated through ArcGIS 10.0 as follows. For each sample plot, we drew a circle of 5 km-radius centred on its barycentre (arithmetic centre of its outline-corners, as calculated by ArcGIS 10.0) and plotted within it a number of random locations equal to the number of real nests censused in that plot (i.e. if a plot contained X nests, we plotted X random locations within its 5 km radial area). The radius of 5 km was chosen because floating, pre-breeding kites frequently prospect 7–10 km wide areas when choosing where to settle to breed (Tanferna et al., 2013; authors' unpubl. GPS-data). Thus, we assumed that each individual could compare the habitat configuration of the location eventually chosen with potential, alternative sites within a 5 km radius, an area that would be easy to observe in its entirety by a high circling kite on a clear day. Once plotted by GIS, we: (1) visited each random location using a handheld GPS; and (2) repositioned the location on the nearest tree or artificial structure judged capable of supporting a kite nest (e.g. with a sufficiently high, solid fork, based on our previous experience in observing hundreds of kite nests).

The variables recorded at each nest or random location are detailed in Supplementary Resource 1 Table A1, they were devised on the basis of our knowledge of local kite ecology,

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and measured vegetation, urban and human features at three "scales". The "nest area" scale estimated the characteristics of the potential nesting tree or artificial structure and its immediate surroundings, such as the height of the nesting structure, woodlot size, or whether the nesting tree was isolated or in a hedgerow, parkland or woodlot (Supplementary Resource 1, Table A1). The "landscape scale" (hereafter "urban scale") measured the urban configuration and landscape structure within 500 m of each sample location, such as indices of road and building density, or percentage and diversity of land-cover types (Supplementary Resource 1, Table A1). It also included the proximity to potentially important features, such as roads, water or rubbish dumps. The 500 m radius was arbitrarily chosen because this is the area around the nest most intensively patrolled for hunting by breeding individuals, especially females, based on intensive observation of focal pairs. Finally, the "human scale" provided direct and indirect estimates of human activities and practices, such as distance to Muslim colonies, efficiency of waste management, or human density. Several of these variables directly or indirectly estimated the potential access of kites to different types of human subsidies, as detailed in Supplementary Resource 2. Nest-area characteristics were measured in the field with a metric tape. Measures of proximity and surface cover, such as distance to roads or woodlot size were assessed in Google Earth Pro and ArcGIS 10.0. Human variables, such as hygiene score or human density, were recorded through ground surveys and interviews with local people (see Supplementary Resource 2 for details).

Statistical Analyses

We used t-tests and χ^2 tests to explore differences between kite nests and random locations. We then employed a mixed model logistic regression (Zuur et al., 2009) with a backward stepwise procedure to examine the nest-area, urban and human factors (Supplementary Resource 1, Table

A1) discriminating between kite nests and random locations. Of the total 308 available locations, we randomly selected 100 nests and 100 random sites for model building, and employed the remaining 54 nests and 54 random locations for model validation (Fielding & Haworth, 1995). Because multiple nests and random locations were drawn from the same plot and its surroundings, and thus were closer to each other than those from other, more distant, sample plots, plot ID was added as a random factor.

To reduce collinearity and the number of variables presented to the logistic regression, we employed the method of variable reduction proposed by Green (1979) and commonly employed in habitat selection studies (e.g. Austin et al., 1996; Soh et al., 2002). In this method, pairs of strongly inter-correlated variables (r > 0.60) are considered as estimates of a single underlying factor, and only one of the two is retained for analysis, usually the one likely to be perceived as more important by the study organism. Collinearity was subsequently checked further by examining the variance inflation factors (VIF) of the explanatory variables, which were always low (< 2; Crawley, 2007; Zuur et al., 2009).

Some of the kites of our study population were GPS-tagged as part of a parallel study on their movement ecology. Because these individuals visited multiple Muslim colonies, and because large numbers of kites (e.g. > 100) were seen to assemble during ritual-feeding episodes, suggesting congregation from distant sites, we decided to estimate the distance of each nest or random location from multiple Muslim colonies. When we compared such distances between nests and random points in exploratory analyses, kites seemed to over-select sites closer than available to the 1st, 2nd and, possibly, 3rd closest colony, after which the difference became unimportant (Supplementary Resource 3). Thus, to provide a comprehensive measure that integrated the proximity to the three nearest Muslim colonies with their human population density (under the assumption that higher rates of refuse and ritualized-feeding should occur in denser colonies), we extracted the first component of a PCA (Tabachnick & Fidell, 1996) run on these four aforementioned variables. It's PC1 (hereafter "access to Muslim subsidies": see Supplementary Resource) explained 65 % of the variance and had a high positive loading on Muslim population density and high negative loadings on the distance to the 1st, 2nd and 3rd closest Muslim colonies. Thus, it provided an increasing index of access to abundant "Muslim subsidies" and was fitted to all models (Supplementary Resource 1, Table A3).

To gain a deeper understanding of habitat quality available to kites, and to test whether the observed habitat choices were adaptive (e.g. Clark & Schutler, 1999; Sergio et al., 2003), we used linear mixed models. These again used plot ID as a random factor and tested the effect of the same set of variables presented to the habitat selection logistic model on both the number of years that a territory was occupied and on the cumulative number of fledglings that it produced between 2013 and 2016. We predict that territories that were more frequently occupied were of higher quality and thus were more attractive to kites, as has been demonstrated in other avian species, including other kite populations (review in Sergio & Newton, 2003).

All multivariate models were built by a frequentist approach through a backward stepwise procedure following Zuur et al. (2009): all explanatory variables were fitted to a maximal model, extracted one at a time from the maximal model, and the associated change in model deviance was assessed by the significance of a likelihood-ratio test; the procedure was repeated until we obtained a final model which only included significant variables (LRT, Zuur et al., 2009). To avoid over-parameterization, we ensured never to fit more than N/3 variables to each maximal model, where N is the sample size of the analyzed dataset (Crawley, 2007). Interactions were fitted only when we had a priori hypotheses about their potential effect, based on our field

observation and knowledge of the population. In particular, we hypothesized that the selection of green cover, urban cover or hygiene level could be conditional upon proximity to Muslim subsidies, because the latter could affect habitat and food profitability. We also hypothesized that the preference for a low level of hygiene (i.e. for high human waste availability) could depend on human density and vice versa, and thus fitted the interaction between hygiene score and human density. Model assumptions were checked by investigating QQ plots, histograms of residuals, and plots of standardized and normalized residuals against fitted values and against explanatory variables (Crawley, 2007; Zuur et al., 2009). All GLMMs were implemented in R.3.0.2 (R Development Core Team 2009). When necessary, variables were logarithmically, or arcsine square root transformed in order to achieve a normal distribution. All tests are twotailed, statistical significance was set at $\alpha < 0.05$, and all means are given ± 1 SE.

2.3. Results

In univariate tests (Supplementary Resource 1, Table A2), at the nest-area scale, kites did not prefer trees over artificial structures, although most nests (87 %) were built in trees. There was also no clear preference for tree species, with kites opportunistically using 13 different tree species (Supplementary Resource 4). Instead, they seemed more selective of the arrangement of trees, over-selecting woodlots and parklands rather than single trees or lines of trees (Fig. 1a). Also, when they nested in woodlots, they selected larger woodlots than the average available (Supplementary Resource 1, Table A2). At the urban scale, kites preferred sites with lower human housing densities, lesser extents of built-up surfaces, higher availability of roads and woodland, and higher habitat diversity (Supplementary Resource 1, Table A2). Finally, kite nests differed from random locations for all human variables. Compared to availability, nests

had higher access to Muslim subsidies, higher density of Muslim inhabitants, higher human density in the streets and greater quantities of anthropogenic refuse (Supplementary Resource 1, Table A2).



Fig. 1. Tree arrangement (Panel a), and index of road density, percentage urban land cover within a 500 m radius, and human density (panel b) at 100 Black Kite nests (black bars) and 100 random locations (white bars) in Delhi (India).



Fig. 2. Urban kites in Delhi selected sites for which access to Muslim colonies and vegetation cover positively covaried (panel a). Thus, they over-selected areas with abundant vegetation close to dense Muslim colonies, but avoided them when far from Muslim colonies (panel b). Access to Muslim colonies was estimated by means of a principal component analysis (see Methods) and portrayed as a categorical progression in panel b for clarity of presentation. Error bars represent 1 SE, black points/bars portray kite nests and white points/bars represent random locations.



Fig. 3. Access to dense Muslim colonies was higher at Black Kite nests (black bars) than at random locations (white bars) when local hygiene levels were high, while inefficient refuse disposal (i.e. low local hygiene) "released" kites from dependency on Muslim ritual subsidies. Error bars represent 1 SE.

According to the logistic model discriminating between kite nests and random locations (Supplementary Resource 1, Table A3a), kites preferentially selected sites in woodland, with higher road density, with less urban cover and greater woodland extent at the landscape scale, with higher human densities in the streets, lower hygiene levels and greater access to Muslim subsidies (Fig. 1 a, b). The interaction of access to Muslim subsidies with hygiene score and with woodland land-cover also entered the model (Supplementary Resource 1, Table A3a): first, low-refuse sites were selected if found close to Muslim colonies, while locations with much refuse were targeted when far from Muslim subsidies (Fig. 3). Second, large woodland extents

were preferred close to Muslim colonies but avoided when far from them (Fig. 3a, b). The logistic model performed well when reapplied on both the training and validation datasets: it correctly reclassified 87 % of the 200 locations used for model building (87 % of 100 nests and 87 % of 100 random sites), and 82 % of the 108 locations set apart for validation (97.4 % of 54 nests and 74.1 % of 54 random sites).

Finally, both territory occupancy and breeding output were higher for territories with higher access to Muslim subsidies, and for those located in parkland and woodland (Supplementary Resource 1, Table A3b, c).

2.4. Discussion

Our study offers a clear example of cities as complex ecosystems that link society and biota at multiple spatio-temporal scales. In particular, integrating human activities and practices with ecological processes at vast spatial scales allowed us to investigate resources which would have otherwise been missed by conventional ecological analyses of urban land-cover. This reinforces the call for improved integration of socio-economic approaches to urban ecology, which will often require a reconceptualization of humans and their activities (Esbjorn-Hargens & Zimmerman, 2009; Grimm et al., 2008; Pickett et al., 2001; Warren & Lepczyk, 2012). Furthermore, the high predictive power of our logistic model of nest-site selection highlighted the importance of habitat models as potential conservation tools for urban planning (for integration of modelling and conservation in urban settings, see examples and reviews in Gordon et al., 2009; Kowarik, 2011; Lepczyk & Warren, 2012; Lerman et al., 2014).

Overall, our model suggested that Delhi Black Kites selected several socio-ecological features at multiple scales, from local tree-arrangement, to neighbourhood-level landscape structure, to the larger-scale spatial zoning of access to subsidies provided by human socio-

religious practices (see below). Thus, the city was not homogenous in its suitability for kites, as might be assumed from their apparently constant presence throughout the city (e.g. Galushin, 1971), which is typical of many facultative scavengers and synurbic species capable of consuming human waste (e.g. Brook et al., 2003; Sorace, 2002). On the contrary, kites avoided monotonously built-up portions of the city and over-selected sites with the following, very specific urban templet.

First, our model suggested that, compared to availability, kites over-selected woodland patches and avoided isolated trees or lines of trees. Woodlots may allow a more favourable micro-climate in a hot tropical city (e.g. Wang et al., 2015). They may also provide higher nestsite availability and thus accommodate a loose kite colony, with consequent potential advantages in turn of conspecific cueing to locate food (e.g. Valone & Templeton, 2002; Danchin et al., 2004), likely to be important in this species (Sergio, 2003; Sergio & Penteriani, 2005) and in this population in particular (see below). The fact that the rate of selection increased from single trees (strongly avoided), to lines of trees (moderately avoided), to parkland (used as available) and then woodland (Fig. 1a) conforms to a progression of attraction to structural arrangements facilitating increasing levels of conspecific proximity. A preference for large patches of parkland and woodland has previously been demonstrated for other raptors inhabiting urban areas (e.g. Hogg & Nilon, 2015; McPherson et al., 2016; Morrison et al., 2016) and confirms the importance of the abundance and arrangement of green vegetation for urban biota (Lepczyk et al., 2017).

Second, while kites avoided high rates of built-up land cover, they simultaneously selected areas with high road and human density. Because human density was assessed in the streets, it equated to an index of human traffic and street-activity, and because refuse is often disposed of

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by people in a disorganized and unpredictable manner in Delhi, high levels of human activity in the streets likely implies more waste accumulation in these areas. This may provide food directly for kites or for co-occurring species that may in turn represent live prey for kites, such as small mammals or pigeons. Thus, kite's habitat decisions seemed to be set not simply on human density per se, which would probably be higher in densely built-up areas (actually avoided), but more specifically on a high density of roads with intense human activity. In this sense, urban configuration was important as it 'structurally' mediated the kites' access to the functionally relevant portion of the human population. In agreement with this interpretation, we have frequently observed hunting kites quartering over roads, or moving through a series of dominant perches, intently 'observing' human traffic in the streets below. Furthermore, the kites' preference for neighbourhoods with less efficient waste management further reinforced the idea that the link with human street-activities was ultimately aimed at refuse exploitation. These analyses confirm the need to integrate conventional variables describing the urban landscape with more direct measures of human activities and practices, as highlighted by various authors (e.g. Alberti, 2008; Grimm et al., 2008; Pickett et al., 2001; Warren & Lepczyk, 2012).

Third, kites over-selected sites that allowed ready access to multiple Muslim colonies, i.e. to concentrations of people whose activities increased the availability of easy food. While several previous studies have investigated the effect of human subsidies on urban taxa, they have usually focused on garden-feeding operated by citizens of the northern hemisphere as a leisure activity (e.g. Cox & Gaston, 2016; Fuller et al., 2012; Lepczyk et al. 2012). In our case, the spatial association of ritualized-feeding with certain religious communities completed the picture of these previous studies by adding a further socio-cultural component, which strongly

characterizes the urban settings of large portions of southern Asia (see also Keniger et al., 2013). In our specific case, the ritual of tossing meat to kites, which is a widespread practice operated daily at predictable public sites, especially among members of the Muslim communities, has probably generated a mosaic of patches with high input of human subsidies. In agreement with this, our GPS-tagged kites regularly visited these sites with very deliberate-directed journeys to them and large numbers of kites, sometimes into the hundreds, were regularly seen to gather quickly during ritual-feeding episodes. However, this high level of congregation may also enhance competition, lowering the predictability of successful access to the subsidy at the individual kite level. This may explain the preference for proximity to multiple Muslim colonies, each one with multiple ritual-feeding sites, as this will allow each individual dozens of daily opportunities to access subsidies. Furthermore, strategic positioning of the nest within 1-2 km of multiple Muslim colonies may allow kites to spot flocks of conspecifics exploiting feeding-rituals, which are conspicuous even to humans, and to join them rapidly through conspecific cueing, as reported for kites in more natural environments (e.g. Sergio, 2003). Note that the ability to exploit sudden flushes of easy food is one of the defining characteristics of this highly opportunistic species even in rural settings (Blanco, 1997; Viñuela, 2000), an ability which may have further pre-adapted it to life in a megacity. The above described coincidence of resource predictability, opportunism, high sociality, and high visibility of conspecific behaviour represents a typical scenario for the evolution of behavioural strategies based on conspecific cueing and attraction (e.g. Danchin et al., 2004; Valone & Templeton, 2002). The advantages described above were confirmed by the higher occupation rate and breeding output of territories in proximity to multiple Muslim colonies, which suggested that these sites were attractive to kites, that they contributed a disproportionate number of fledglings to the

population, and that the observed habitat choices were adaptive in terms of offspring production (i.e. over-selection of sites which offer a reproductive reward).

Fourth, the importance of strategic proximity to Muslim colonies was further confirmed by its interaction with other habitat features. Compared to a random distribution, kites overselected sites for which green cover and access to Muslim colonies covaried positively (Fig. 2a). This implied that, close to Muslims, kites preferred neighbourhoods with abundant green cover, which may accommodate more nests and facilitate colony-formation, with potential benefits in terms of conspecific cueing (e.g. being alerted of the start of feeding-rituals by the departure of nearby conspecifics). Ultimately, this should allow density to be fine-tuned on food availability (larger densities close to large food concentrations). On the contrary, in scenarios of low food availability (low access to Muslim colonies, Fig. 2b), kites preferred sites with low green cover, which will limit density, thus lowering competition for limited food. Furthermore, the preference for proximity to Muslim colonies was especially pronounced in neighbourhoods where human refuse was scarce (Fig. 3). When hygiene levels were already low, food was likely available in the immediate nest surroundings, allowing kites to be less dependent on Muslim colonies and to nest farther from them. These results suggest that (a) access to hotspots of ritualized-feeding modulated the suitability of other habitats, even when these were located kilometres away from such sites, which functionally integrated far-away components of the urban ecosystem (see also Alberti, 2008; Grimm et al., 2000); (b) ritualized subsidies and waste production/disposal seemed to be the two pillars that directly or indirectly permeated all habitat preferences; and (c) kites seemed to strategically balance their access to these two factors in their habitat choices.

Overall, kite habitat decisions were tightly intertwined with human activities. They preferred sites with extensive access to roads busy with humans, with inefficient waste management and ready access to ritual cultural practices conducive to food subsidies. To date, humans have often been seen as obstacles, threats or nuisances that animal species have to deal with in order to 'tolerate' urbanization (e.g. Chace & Wash, 2006; McPherson et al., 2016; Soh et al., 2002). However, for many urban species, the attraction to an extreme anthropogenic ecosystem is based on the exploitation of human provision itself rather than resilience to its actions, and for some synanthropic species this may derive from millennia of co-existence with man, better seen as an integral portion of their niche as well as a beneficiary of ecosystem services (e.g. Gangoso et al., 2013; Marzluff & Angell, 2005). In our system, Delhi kites cannot be thought of in isolation from humans and their voluntary and involuntary subsidies, which would qualify them as anthropophilic and anthropo-dependent species (sensu Hulme-Beaman et al., 2016). While the importance of human subsidies in altering the mosaic of foraging opportunities for animals is well appreciated (Fuller et al., 2012; Lepczyk et al., 2012; Newsome et al., 2014; Oro et al., 2013), in our case, the subsidy-mosaic was uniquely tied to a complex array of human themes, such as (1) the Indian-level and local-level history of Muslim displacements, which followed India's independence and which determined the current distribution of Muslim colonies;

(2) the global economy that drives urban sprawl, as well as the local economics of trade, which influenced the stability of some historical Muslim colonies; (3) the municipal planning of the currently skyrocketing urban expansion, which affects road and vegetation arrangement, as well as the efficiency of refuse disposal; and (4) the temporal dynamicity of cultural and religious practices, such as ritualized-feeding, which originated among Hindus but is currently prevalent among Muslim groups (e.g. Gupta, 1998; Paul & Nagendra, 2015; Pinault, 2008; Sharan, 2014;

Taneja, 2015). All the above tied kites' habitat choices to the spatial end-results of human activities shaped by history, socio-economics, politics, tradition and religion. Also, these links acted at time scales ranging from decades to centuries and at spatial scales ranging from neighbourhood to global. We believe that similarly tight and complex relations will apply to many other synurbic species worldwide (Francis & Chadwick, 2012).

2.5. Conservation implications

The preference for certain amounts and configurations of woodland makes room for potential modulation of kite density through urban planning, as proposed for crows in Singapore (Soh et al., 2002). For example, promotion of woodlots close to areas with problematic refuse disposal may improve the potential ecological service provided by kite consumption of organic waste, a benefit that could be confirmed through adaptive management. Over the longer-term, waste disposal will be likely rationalized, mechanized and often processed indoor, as progressively legally enforced in developed countries. This will likely imply major declines in kite food availability, which could be partly buffered by planned maintenance and promotion of ritual feeding practices, seen as a unique connection between human culture and ecological function in rapidly expanding urban ecosystems (see below).

The close connection of urban kites to human activities, and their wide-ranging behaviour, typical of mobile avian predators, which tied them to far away sectors of the city, make them an ideal indicator species that integrates processes occurring at different scales of the urban landscape. In particular, the dependency of an urban top predator on ritual feeding, human culture and religion, which promotes one of the largest predator concentrations in the world (Kumar et al., 2014), could be seen as a socio-cultural and ecological uniqueness that connects
urban dwellers with nature and has to be attentively preserved, just as an urban green space. In this context, investigation and documentation of the socio-historical aspects and ecological implications of ritual feeding should be actively promoted.

As any megacity, Delhi is likely to change rapidly in coming decades in terms of sprawl, internal structure, management and culture (Grimm et al., 2008; Sharan, 2014; Srivastava, 2015). Modernization will sooner or later rationalize refuse disposal and younger generations already seem less interested in cultural practices such as ritualized-feeding (authors unpubl. data), which will imply major shifts in resource availability and a threat to a unique system of human-predator coexistence. Such conundrums between modernization, improving human conditions and protecting unique eco-cultural treasures such as the ritual feeding of kites will be formidable challenges to urban planning for innumerable, fast-growing towns and cities of the developing world (e.g. Gangoso et al., 2013).

Acknowledgements

We thank Prof. Nilon and two anonymous reviewers for constructive comments on an earlier draft of the manuscript. We are grateful to Ben Sheldon, Chris Perrins, Tommaso Pizzari, Ujiwal Kumar, L. Agarwal and the Director, Dean and Research Coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Civic bodies of the Government of NCT of Delhi helped with legal permits, and Mr. A. Agnihotri, Director of the National Zoological Park of New Delhi provided accommodation and gave permission to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We express our most heartfelt gratitude to N. Shehzad and M. Saud of Wildlife Rescue for providing essential information, and to all the volunteers of the "Black Kite Project Group" from the University of Delhi (Sri Venkateswara and Deshbandhu Colleges), especially R. Prajapati, R. Negi, B. Sharma, P. Kumar and M. Singh who provided essential field help, enthusiasm and cooperation in the environmental education of locally assembling crowds of curious people. Special thanks to our field assistant Laxmi Narayan, who was the backbone of the field team. Finally, thanks to all the landowners, managers and government officials who patiently cooperated with our constant requests of access. The project was funded through grants by the Raptor Research and Conservation Foundation (Mumbai) and by the Govt. of India, Ministry of Environment, Forest and Climate Change. N Kumar's D. Phil at the University of Oxford was funded by the Felix Scholarship Trust. Funding for travelling and fieldwork by F. Sergio was afforded by Project RNM-7307 of the Junta de Andalucía and CGL2015- 69445-P of the Spanish Ministry of Economy and Competitiveness.

References

Alberti, M. (2008) Advances in urban ecology: integrating humans and ecological processes in urban ecosystems. *Springer*, New York.

Anonymous (2016) Rise of the city. Science 352: 906-907

- Austin, G.E., Thomas, C.J., Houston ,D.C., & Thompson, B.A. (1996) Predicting the spatial distribution of buzzards *Buteo buteo* nesting areas using a Geographical Information System and remote sensing. *Journal of Applied Ecology* 33: 1541-1550
- Belant, J.L. (1997) Gulls in urban environments: landscape-level management to reduce conflict. *Landscape and Urban Planning* 38: 245-258.
- Blanco, G. (1997) Role of refuse as food for migrant, floater and breeding Black Kites (*Milvus migrans*). Journal of Raptor Research 31: 71-76
- Brook, B.W., Sodhi, N.S., Soh, N.C.K., & Chuam, Lim H. (2003) Abundance and projected control of invasive house crows in Singapore. Journal of Wildlife Management 67: 808-817.
- Carey, M.P., Sanderson, B.L., Barnas, K.A., & Olden, J.D. (2012) Native invaders: Challenges for science, management, policy, and society. Frontiers in Ecology and Environment 10: 373-381
- Chace, J.F., & Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landscape and Urban Planning* 74: 46-49
- Champion, H.G., & Seth SK (1968) A Revised Survey of the Forest Types of India. *Manager* of *Publications, Government of India*, New Delhi.
- Clark, R.G., & Schutler, D. (1999) Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology* 80: 272-287
- Cox, D.T.C., & Gaston, K.J. (2016) Urban bird feeding: connecting people with nature. *PLoS ONE* 11 (7), e0158717, doi:10.1371/journal.pone.0158717
- Crawley, M.J. (2007) The R Book. Wiley Press, Chichester.

- Danchin, É., Giraldeau, L., Valone, T.J., & Wagner, R.H. (2004). Public Information: from noisy neighbors to cultural evolution. *Science* 305: 487-491.
- Esbjorn-Hargens, S., & Zimmerman, M.E. (2009) Integral Ecology: uniting multiple perspectives on the natural world. *Integral Books*.
- Evans, K.L., Chamberlain, D.E., Hatchwell, B.J., Gregory, R.D., & Gaston, K.J. (2011) What makes an urban bird? *Global Change Biology* 17: 32-44
- Fielding, A.H., & Haworth, P.F. (1995) Testing the generality of bird-habitat models. *Conservation Biology* 9: 1466-1481
- Francis, R.A., & Chadwick, M.A. (2012) What makes a species synurbic? *Applied Geography* 32: 514-521
- Fuller, R.A., Irvine, K.N., Davies, Z.G., Armsworth, P.R., & Gaston, K.J. (2012) Interactions between people and birds in urban landscapes. *Avian Biology* 45: 249-266
- Galushin, V.M. (1971) A huge urban population of Birds of prey in Delhi India. Ibis 113: 522
- Gangoso, L., Agudo, R., Anadón, J.D., dela Riva, M., Suleyman, A.S., Porter, R., & Donázar, J.A. (2013) Reinventing mutualism between human san wild fauna: insights from vultures as ecosystem services providers. *Conservation Letters* 6: 172-179
- Green, R.H. (1979) Sampling design and statistical methods for environmental biologists. *John Wiley and Sons*, New York.
- Grimm, N.B., Steward, J.M.G., Pickett, T.A., & Redman, C.L. (2000) Integrated approaches to long-term studies of urban ecosystems. *BioScience* 50: 571-584
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., & Briggs, J.M. (2008) Global change and ecology of cities. *Science* 319: 756-760
- Gupta, N. (1998) Delhi between two empires, 1803–1931: society, government, and urban growth. *Oxford University Press*, New Delhi.
- Hogg, J.R., & Nilon, C.H. (2015) Habitat associations of birds of prey in urban business parks. *Urban Ecosystems* 18: 267–284.

- Hosey, G., & Melfi, V. (2014) Human-animal interactions, relationships and bonds: a review and analysis of the literature. *International Journal of Comparative Psychology* 27: 117-142
- Hulme-Beaman, A., Dobney, K., Cucchi, T., & Searle, J. B. (2016). An ecological and evolutionary framework for commensalism in anthropogenic environments. *Trends in* ecology & evolution, 31(8), 633-645.
- Inger, R., Cox, D. T., Per, E., Norton, B. A., & Gaston, K. J. (2016). Ecological role of vertebrate scavengers in urban ecosystems in the UK. *Ecology and evolution*, *6*(19), 7015-7023.
- Keniger, L. E., Gaston, K. J., Irvine, K. N., & Fuller, R. A. (2013). What are the benefits of interacting with nature?. *International journal of environmental research and public health*, 10(3), 913-935.
- Kirmani, N. (2016). *Questioning the 'Muslim Woman': Identity and Insecurity in an Urban Indian Locality.* Routledge India.
- Kowarik, I. (2011). Novel urban ecosystems, biodiversity, and conservation. *Environmental pollution*, *159*(8-9), 1974-1983.
- Kumar, N., Mohan, D., Jhala, Y. V., Qureshi, Q., & Sergio, F. (2014). Density, laying date, breeding success and diet of Black Kites Milvus migrans govinda in the city of Delhi (India). *Bird study*, 61(1), 1-8.
- Kurosawa, R., Kanai, Y., & Matsuda, M. (2003) Conflict between Human and Crows in Greater Tokyo. *Global Environmental Research* 7: 139-147.
- Lepczyk, C.A., & Warren, P.S. (2012) Urban bird ecology and conservation. University of California Press.
- Lepczyk, C.A., Warren, P.S., Machabée, L., Kinzig, A.P., & Mertig, A.G. (2012) Who feeds the birds? A comparison across regions. In: Urban bird ecology and conservation (Eds. CA Lepczyk, PS Warren), pp. 267-286, University of California Press.
- Lepczyk, C.A., Aronson, M.F.J, Goddard M.A., Lerman S.B.,& MaIvor, J.S. (2017) Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. BioScience 67: 799-807.

- Lerman, S.B., Nislow, K.H., Nowak, D.J., DeStefano, S., King, D.I., Jones-Farrand, T. (2014) Using urban forest assessment tools to model bird habitat potential. Landscape and Urban Planning 122: 29–40.
- Liu, J., Dietz, T., Carpenter, S. R., Alberti, M., Folke, C., Moran, E., ... & Ostrom, E. (2007). Complexity of coupled human and natural systems. *science*, *317*(5844), 1513-1516.
- Magle, S. B., Hunt, V. M., Vernon, M., & Crooks, K. R. (2012). Urban wildlife research: past, present, and future. *Biological conservation*, *155*, 23-32.
- Malakoff, D., Wigginton, N. S., Fahrenkamp-Uppenbrink, J., & Wible, B. (2016). Rise of the urban planet. *Science*. http://www.sciencemag.org/news/2016/05/rise-urban-planet. [Accessed 12.10.16]
- Marzluff, J. M. (2017). A decadal review of urban ornithology and a prospectus for the future. *Ibis*, *159*(1), 1-13.
- Marzluff, J. M., & Angell, T. (2005). Cultural coevolution: how the human bond with crows and ravens extends theory and raises new questions. *Journal of Ecological Anthropology*, 9(1), 69-75.
- Marzluff, J. M., McGowan, K. J., Donnelly, R., & Knight, R. L. (2001). Causes and consequences of expanding American Crow populations. In *Avian ecology and conservation in an urbanizing world* (pp. 331-363). Springer, Boston, MA.
- Mayer, P. (2010). Urban ecosystems research joins mainstream ecology. *Nature*, 467(7312), 153-154.
- McKinney, M.L. (2010) Urbanization, biodiversity, and conservation. BioScience 52: 883-890
- McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127: 247-260
- McPherson, S. C., Brown, M., & Downs, C. T. (2016). Crowned eagle nest sites in an urban landscape: Requirements of a large eagle in the Durban Metropolitan Open Space System. *Landscape and Urban Planning*, 146, 43-50.
- Moleon, M., Sanchez-Zapata, J. A., Margalida, A., Carrete, M., Owen-Smith, N., & Donazar, J. A. (2014). Humans and scavengers: the evolution of interactions and ecosystem services. *BioScience*, 64(5), 394-403.

- Morrison, J. L., Gottlieb, I. G., & Pias, K. E. (2016). Spatial distribution and the value of green spaces for urban red-tailed hawks. *Urban ecosystems*, *19*(3), 1373-1388.
- Naoroji, R. (2006). Birds of prey of the Indian subcontinent. Christopher Helm.
- Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J., & Dickman, C. R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, 24(1), 1-11.
- Nilon, C. H. (2011). Urban biodiversity and the importance of management and conservation. *Landscape and ecological engineering*, 7(1), 45-52.
- Oro, D., Genovart, M., Tavecchia, G., Fowler, M. S., & Martínez-Abraín, A. (2013). Ecological and evolutionary implications of food subsidies from humans. *Ecology letters*, 16(12), 1501-1514.
- Parker, T. S., & Nilon, C. H. (2012). Urban landscape characteristics correlated with the synurbization of wildlife. *Landscape and Urban Planning*, 106(4), 316-325.
- Paul, S., & Nagendra, H. (2015). Vegetation change and fragmentation in the mega city of Delhi: Mapping 25 years of change. *Applied Geography*, 58, 153-166.
- Pickett, S. T., Cadenasso, M. L., Grove, J. M., Nilon, C. H., Pouyat, R. V., Zipperer, W. C., & Costanza, R. (2001). Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Annual review of ecology and systematics*, 32(1), 127-157.
- Pinault, D. (2008) Raw meat skyward: Pariah-kite rituals in Lahore. In: Comparative Islamic studies: notes from the fortune-telling parrot: Islam and the struggle for religious pluralism in Pakistan (Ed. D. Pinault), pp. 108-121, Equinox Publishing Ltd, Bristol, CT, USA.
- Sergio, F. (2003) From individual behavior to population pattern: weather-dependent foraging and breeding performance in Black kites. *Animal Behaviour* 66: 1109-1117
- Sergio, F. & Newton, I. (2003) Occupancy as a measure of territory quality. *Journal of Animal Ecology* 72: 857-865
- Sergio F, Pedrini P, Marchesi L (2003) Spatio-temporal shifts in gradients of habitat quality for an opportunist avian predator. Ecography 26: 243-255.

- Sergio, F., Pedrini, P., & Marchesi, L. (2003). Spatio- temporal shifts in gradients of habitat quality for an opportunistic avian predator. *Ecography*, *26*(2), 243-255.
- Sharan, A. (2014). In the City, Out of Place: Nuisance, Pollution, and Dwelling in Delhi, C. 1850-2000. *OUP Catalogue*.
- Shochat, E., Lerman, S. B., Anderies, J. M., Warren, P. S., Faeth, S. H., & Nilon, C. H. (2010). Invasion, competition, and biodiversity loss in urban ecosystems. *BioScience*, 60(3), 199-208.
- Soh, M. C., Sodhi, N. S., Seoh, R. K., & Brook, B. W. (2002). Nest site selection of the house crow (Corvus splendens), an urban invasive bird species in Singapore and implications for its management. *Landscape and Urban Planning*, 59(4), 217-226.
- Sorace, A. (2002). High density of bird and pest species in urban habitats and the role of predator abundance. *Ornis Fennica*, 79(2), 60-71.
- Soulsbury, C. D., & White, P. C. (2015). Human–wildlife interactions in urban areas: a review of conflicts, benefits and opportunities. *Wildlife Research*, 42(7), 541-553.
- Srivastava, S. (2014). Entangled urbanism: Slum, gated community and shopping mall in Delhi and Gurgaon. *OUP Catalogue*.
- Tabachnick, B.G. & Fidell, L.S. (1996) Using multivariate statistics. HarperCollins, New York.
- Taneja, A. V. (2015). Saintly animals: the shifting moral and ecological landscapes of North India. *Comparative Studies of South Asia, Africa and the Middle East*, *35*(2), 204-221.
- Tanferna, A., López-Jiménez, L., Blas, J., Hiraldo, F., & Sergio, F. (2013). Habitat selection by Black kite breeders and floaters: Implications for conservation management of raptor floaters. *Biological Conservation*, 160, 1-9.
- United Nations, Department of Economic and Social Affairs, Population Division (2015). *World Urbanization Prospects*: The 2014 Revision, (ST/ESA/SER.A/366)
- Valone, T. J., & Templeton, J. J. (2002). Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 357(1427), 1549-1557.

- Viñuela, J. (2000) Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. *Behavioural Ecology and Sociobiology* 48: 333–343
- Wang, Y., Bakker, F., de Groot, R., Wortche, H., & Leemans, R. (2015). Effects of urban trees on local outdoor microclimate: synthesizing field measurements by numerical modelling. *Urban ecosystems*, 18(4), 1305-1331.
- Warren, P. S., & Lepczyk, C. A. (2012). Beyond the gradient: insights from new work in the avian ecology of urbanizing lands. Urban bird ecology and conservation. University of California Press, Berkeley, 1-6.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). GLM and GAM for count data. In *Mixed effects models and extensions in ecology with R* (pp. 209-243). Springer, New York, NY.

Principal Component 1: Increasing access to Ritual subsidies

NEST LOCATION

RANDOM LOCATION



(+) ve load of # people & (-) ve loading of distance to an old colony

A schematic depicting the Principal Component 1 extracted by using four independent variables: number of Muslims within a 2000 m radial area, and three successive distances to the Muslim pockets (colonies) from the point location (nest/random point). (Chapter 2,3,4 & 5).



A schematic depicting the mechanism of evolution of habitat selection by the breeding Black Kites in an urban habitat (Chapter 2 and 5). Note that the funnel and water droplet have been used to depict an analogy.

Supplementary Resource 1

Variable	Description	
Nest-area scale:		
Nest substrate	0 = tree; 1 = artificial structure (pylon, metal tower, electricity pole, building)	
Nest tree species	Species of the nesting tree	
DBH (cm)	Diameter of the tree trunk at 1.4 m above the ground	
Tree or pylon height (m)	Height of the nesting tree or artificial structure	
Nest height (m)	Height of the nest above the ground	
Tree arrangement	Categorical variable: $1 = \text{isolated tree/pylon}$; $2 = \text{line of trees (e.g. along an avenue)}$; $3 = \text{parkland (scattered trees with > 5-10 m of open ground between them, typically grassland in urban parks)}; 4 = \text{woodlot}$	
Woodlot Size (ha)	Size of the woodlot (only for locations classed as 4 above)	
Urban scale: landscape structure and composition		
Index of buildings' density	Number of buildings crossed by a 500 m north-south and a 500 m east-west transect crossing each other on the nest/random location	
Index of road density	Number of asphalted roads crossed by a 500 m north-south and a 500 m east-west transect crossing each other on the nest/random location	
Urban cover	Percentage area covered by built-up structures (buildings, roads, parking lots, or any other impervious surface) within 500 m of the nest/random location	
Green cover	Percentage area covered by shrub/tree vegetation within 500 m of the nest/random location	
Open habitats	Percentage area free of built-up structures or arboreal vegetation within 500 m of the nest/random location (e.g. water, grassland, cultivated fields, rocky outcrops etc).	
Habitat diversity	Shannon-Wiener index of habitat diversity based on the three land cover variables above	
Distance to road (m)	Distance to the nearest asphalted road	

Table A1: Environmental variables measured at Black Kite nests and random locations in Delhi (India).

Distance to water (m)	Distance to the nearest water body
Distance to illegal dump (m)	Distance to the nearest illegal dump (self-created by citizens, not recognized by any local municipality and often present only for a limited period of time)
Distance to landfill (m)	Distance to the nearest, large, authorized refuse dump
Human scale: variables characterising	
human presence, practices and activities	
Historical setting	Categorical variable: 0 = more recently built portion of the city (New Delhi); 1 = older, more historical portion of the city (Old Delhi).
Hygiene score	Level of sanitation: 1 = clean areas; 2 = areas under poor waste management regimes
Human density	Average number of people walking within 2m of a stationary observer during 5 min at 10 locations randomly plotted within 200 m of the nest/random location 4
Muslim Density	Estimate of the local density of Muslim inhabitants (see details of calculations in Appendix B)
Access to Muslim subsidies	First component PC1 of a principal component analysis on Muslim density and the proximity to the three closest Muslim colonies

•For locations on artificial structures, the DBH of the structure was estimated as the value predicted (given its height) by a regression of tree height on DBH (calculate on tree-sites only).

Old Delhi has a higher abundance of old buildings, a higher share of Muslim population and a higher concentration of slaughterhouses and meat selling shops than the more recently built portion of the city. Thus, it may represent a macro-portion of the city with higher availability of human subsidies (details in Online Resource 2).

 \circ Categorical variable with two levels: 1 = efficient waste disposal with very scarce or no organic refuse in the streets; 2 = abundant and widespread refuse in the streets throughout the area, either in small frequent piles, in illegal ephemeral dumps, or as individual items scattered a bit of everywhere through all streets (see also Appendix B).

^a Counts were only operated between 10:00-17:00 hrs and avoided during atypical, momentary peak periods of human traffic, such as exits from work or schools, in order to maintain consistency across sites (details in Online Resource 2)

Supplementary Resource 1

Table A2: Mean (± 1 SE) estimates of variables measured at 100 Black Kite nests and at 100 randomly chosen locations in Delhi, India. Differences between the two samples were tested by means of t-tests, or χ^2 tests for categorical variables. Symbols: * P < 0.05; ** P < 0.01; *** P < 0.001.

Variable	Nest Sites	Random Locations	
Nest-area scale:			
Nest substrate ^{a, b}	88.31 %	80.52 %	
DBH (cm) ^b	75.47 ± 2.97	68.86 ± 2.43	
Tree or pylon height (m)	14.86 ± 0.72	15.62 ± 0.52	
Nest height (m) ^b	11.86 ± 0.63	12.06 ± 0.54	
Woodlot size (ha) ***	17.47 ± 2.67	2.89 ± 1.78	
Urban scale:			
Index of buildings' density b ***	18.85 ± 1.52	27.45 ± 1.75	
Index of road density ^b ***	7.12 ± 5.33	5.33 ± 0.26	
Urban cover ^b ***	0.38 ± 0.02	0.53 ± 0.02	
Green cover ^b ***	0.28 ± 0.02	0.19 ± 0.01	
Open habitats	0.33 ± 0.02	0.28 ± 0.02	
Habitat diversity ^b ***	0.96 ± 0.02	0.85 ± 0.02	
Distance to road $^{b}(m)$	81.33 ± 9.72	79.91 ± 8.41	
Distance to water b (m)	220.32 ± 30.39	275.29 ± 22.62	
Distance to illegal dump ^b (m)**	717.08 ± 68.20	435.43 ± 46.82	
Distance to landfill ^b (m)	6964.70 ± 318.42	7175.70 ± 355.44	
Human scale:			
Historical setting ^c ***	71 %	38 %	
Hygiene score ^{b, d} *	66.23 %	50.65 %	
Human density ^b ***	12.96 ± 0.97	7.28 ± 0.65	
Muslim Density **	32223 ± 2552.13	21296 ± 2231.5	
Access to Muslim subsidies ^b **	$0.25 \pm .09$	-0.17 ± 0.1	

^a Percent of nest / random locations on trees.

^b Variable that was fitted to the multivariate models of Table A3.

^c Percent of nest / random locations located in Old Delhi.

^d Percentage of locations with poor sanitation.

Supplementary Resource 1

Table A3: Logistic regression (a) and linear mixed models (b, c) testing the effect of environmental and human variables on nest site selection (a), territory occupancy (b) and offspring production (c). Plot identity was added as a random factor to all models (see Methods).

Variable		$B \pm SE$	Z-test	<i>P-</i> value
a.	Dependent variable: nest-site selection ^{a,b}			
	(N = 100 nests vs 100 random locations)			
	Tree arrangement (tree line) ^c	0.26 ± 0.74	0.35	0.729
	Tree arrangement (parkland) ^c	1.65 ± 0.69	2.41	0.015
	Tree arrangement (woodland) ^c	2.94 ± 0.86	3.43	< 0.001
	Index of road density	0.34 ± 0.11	3.10	0.002
	Urban cover	-7.18 ± 2.06	-3.50	< 0.001
	Green cover	-1.00 ± 2.88	-0.34	0.731
	Human density	0.17 ± 0.05	3.33	< 0.001
	Hygiene score	2.38 ± 0.63	3.78	< 0.001
	Access to Muslim subsidies	-0.33 ± 1.06	-0.31	0.758
	Access to Muslim subsidies * Green cover	8.55 ± 2.87	2.98	0.003
	Access to Muslim subsidies * Hygiene score	-2.02 ± 0.80	-2.53	0.011
	Intercept	-3.24 ± 1.64	-	-
b.	Dependent variable: occupancy ^d (N = 153 ^e)			
	Tree arrangement (tree line) ^c	0.20 ± 0.28	0.72	0.471
	Tree arrangement (parkland) ^c	0.52 ± 0.20	2.56	0.011
	Tree arrangement (woodland) ^c	0.35 ± 0.22	1.59	0.111
	Access to Muslim subsidies	0.14 ± 0.07	2.11	0.035
	Intercept	0.43 ± 0.19	-	-
c.	Dependent variable: fledglings produced in			
	four years $f(N = 153^{\circ})$			
	Tree arrangement (tree line) ^c	0.09 ± 0.36	0.26	0.798
	Tree arrangement (parkland) ^c	0.74 ± 0.25	2.95	0.003
	Tree arrangement (woodland) ^c	0.23 ± 0.27	0.87	0.384
	Access to Muslim subsidies	0.28 ± 0.08	3.51	< 0.001
	Intercept	0.03 ± 0.23	-	-

^a Generalised linear mixed model with binomial errors and a logit link function. The model discriminated between 100 kite nests and 100 random locations.

^b Variables presented to the model: Nest substrate, DBH, Tree or pylon height, Nest height, Tree arrangement, Woodlot size, Index of building density, Index of road density, Urban cover, Green cover, Habitat diversity, Distance to road, Distance to water, Distance to illegal dump, Distance to landfill, Hygiene score, Human density, Access to Muslim subsidies, Access to Muslim

subsidies*Urban cover, Access to Muslim subsidies*Green cover, Access to Muslim subsidies*Hygiene score, Human density*Hygiene score (details of the rationale for fitting interactions an be found in the Methods). Variables of Table A1 not presented to the model to avoid collinearity: Open habitats, Historical setting.

^c Categorical variable with four levels: 1 = isolated tree/pylon, 2 = line of trees, 3 = parkland, 4 = woodlot.

^d Generalised linear mixed model with Poisson errors and a logit link function. The dependent variable is the number of years that a territory was occupied, which ranged from 1 to 4.

^e One territory (of the overall sample of 154 territories used for building the nesting habitat selection model) could not be sampled after the first year for logistic reasons (inability to access a private property). Thus, the occupancy and breeding success models were based on a sample of 153 territories, each sampled in all the four years of investigation.

^f Generalised linear mixed model with Poisson errors and a logit link function. The dependent variable is the number of young raised to fledging age in four years, which ranged from 0 to 9.

Supplementary Resource 2

Access to human subsidies by Delhi kites: rationale and estimation

In Delhi, kites obtain their main food (meat waste from humans, Kumar et al., 2014) from three major sources: (1) dump (garbage landfill) sites, although these are mainly used by nonbreeding kites; (2) roads, especially those with a high density of commercial activities and families, who often dispose their personal waste by leaving it directly in the streets, which may in turn attract potential complementary live prey for kites, such as rodents or pigeons (Kumar et al., 2014, authors' unpublished nest camera-trapping data); (3) direct and indirect effects of religio-cultural practices, such as the higher abundance of meat selling shops and the ritualizedfeeding by people who follow Islamic faith in Muslim colonies and in the older establishments of the city (Old Delhi). Thus, because direct, quantitative measurements of such capillarydistributed subsidies would be impossible over such large areas, we considered that proximity to dump sites, local human density in the streets, and religious zoning could be potential surrogates of kite food availability. Therefore, for each nest or random location, we calculated the following variables. (1) First, we measured the distance to the nearest legal or illegal refuse dump site. Such dumps were easily located during our fieldwork on the basis of frequent observation of unauthorized disposal of garbage at certain sites of each plot, where piles of refuse accumulated in evident manners. (2) Second, human traffic and density in the streets was

estimated by counting for five minutes the number of people who passed by a stationary observer at 5-10 randomly plotted locations (depending on local conditions, e.g. less points in rural plots with few roads) along the roads within a circle of 200 m centred on each nest or random location. To standardize them as much as possible in relation to human activities, these counts were operated exclusively during working days and between 1000 - 1700 hrs, and halted during unusual events that could have biased the estimates (e.g. sudden exit from work or local schools). (3) Third, we interviewed 10 random people in the streets around the nests and random locations about the routine removal of garbage from the local dumps, and integrated it with our own observations of local conditions to create a hygiene index, which classed sites as relatively clean with little litter in the streets and constantly low refuse availability for kites, or as more dirty, with constant presence of large garbage piles in the streets, or in close proximity to stable rubbish dumps (Supplementary Resource 1). (4) Fourth, in the absence of fine-scale data on human population density by religion, we estimated the number of inhabitants of Muslim faith within a 2 km circle centred on each nest or random location in the following manner. First, we extracted the number of Muslim inhabitants for each sub-district of the city, using the 2011 census data (http://censusindia.gov.in/2011census). Second, we digitized the areal extent of Muslim colonies in each sub-district using Google Earth Pro Imagery and our own ground visits to such colonies. Third, we divided the Muslim population of each sub-district by the area of Muslim colonies within each sub-district to obtain a gross estimate of local Muslim density/unit area, under the assumption that the majority of the Muslim population was concentrated at such "closed" colonies (as supported by well-known and widespread religious ghettoization in India: see Gupta (1998) and Kirmani (2013) for details). Fourth, we multiplied such local density by the actual area of Muslim colonies included in each 2 km-circle, so as to re-adapt the sub-district level Muslim density to the circle around each nest or random location. (5) Finally, we classed locations as placed in the old section of the city (Old Delhi) or within the more recently built up areas (New Delhi). These two categories represented macro-areas under different forms of urbanization history and intensity, configuration, and hygiene, Old Delhi including a large share of Muslim colonies with poor sanitation as well as high concentrations of meat shops.

Supplementary Resource 3

Mean distance to Muslim colonies for 100 Black Kite nests (black bars) and 100 random locations (white bars) in Delhi (India). The difference between kite nests and random locations was significant for the first and second closest Muslim colony, and marginally significant for the third closest Muslim colony, suggesting over-selection of sites close to multiple sources of ritual subsidies. Symbols: ** P < 0.01; + P < 0.1. Error bars represent 1 SE.



Muslim colony

Supplementary Resource 4

Proportional incidence of tree species among kite nests and random locations in Delhi. There was no significant over-selection or avoidance by kites of main tree species type ($\chi^2 = 6.15$, P = 0.104). The category "Other tree species" incorporated all tree species which occurred less than 5 times among kite nests or random locations and included the following species: Honey mesquite *Prosopis juliflora* (N = 12 for nests and 0 for random locations), Jamun *Syzygium cumini* (10, 1), Semal *Bombax ceiba* (4, 8), Devil's tree *Alstonia scholaris* (3, 4), Indian rosewood *Dalbergia sissoo* (3, 3), Gulmohar *Delonix regia* (2, 0), Siris *Albizia lebbeck* (0, 2), Mango *mangifera indica* (1,1), Cottonwood *Populus gamblei* (1, 1), Dinner Plate tree *Pterospermum acerifolium* (1,0), Monkeypod *Pithecellobium dulce* (0, 1), Unidentified (2, 3).



Tree type

Offspring defense by an urban raptor responds to human subsidies and ritual animal-feeding practices

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Originally published on October 29, 2018; Volume 13(10), PLoS ONE.

• <u>Published typesetting included in the Appendix</u>

Abstract

There is a growing interest in the behavioural and life history mechanisms that allow animal species to cope with rapidly expanding urban habitats, which impose frequent proximity to humans. A particular case of behavioral bottleneck (i.e. conflicting interests) faced by animals in urban environments is how they will modulate the defence of their offspring against the potential danger represented by humans, an aspect that has received scarce research attention. We examined the nest defense against humans by a dense breeding population of a raptor, the Black Kite Milvus migrans, within the megacity of Delhi (India). Here, kites live on a diet dominated by human waste and meat offered through religiously motivated bird feeding practices. Nest defense levels increased with the number of offspring, and with the progression of the breeding season. Defense also intensified close to ritual-feeding areas and with increasing human waste in the streets, suggesting synergistic effects of food availability, parental investment, personality-boldness and habituation to humans, with consequent attenuation of fear. Thus, the behavioural response to a perceived threat reflected the spatial mosaic of activity of humans in the city streets, their cultural practices of ritual-feeding, and their wastemanagement. For synurbic species, at the higher-end spectrum of adaptation to an urban life, human cultural practices and attitudes may well be the most defining dimensions of their urban niche. Our results suggest that, after initial urban colonization, animals may continue to adapt to the typically complex, heterogeneous environments of cities through fine-grained behavioural adjustments to human practices and activities.



A schematic depicting the three ordinal increasing levels of offspring defence by the resident Black Kite race (Chapter 3 & 4).

3.1. Introduction

Rapid, worldwide urbanization is raising interest in urban ecology and in the ways animals adapt to novel and burgeoning urban environments (McDonnell & Hahs, 2015). In particular, behavioural mechanisms that mediate such adaptation remain an under-researched topic (Hahs & Evans, 2015; Miranda et al., 2013), with current knowledge mostly limited to a handful of species that have only recently colonized or are in the process of capitalizing on urban environments e.g. (Chamberlain et al., 2009; Evans et al., 2010; Miranda et al., 2013). Furthermore, these species have typically been studied in biogeographic regions with a long history of wildlife persecution by humans, whose proximity is frequently seen as a potential obstacle for urban colonization e.g. (Lowry et al., 2013; Smart et al. 2010). For example, many studies have focused on flight initiation distances (FID) to explore how behavioural characteristics or personality features may allow certain individuals to better cope with proximity to humans in highly anthropogenic environments (Blumstein, 2006; Carrete & Tella, 2011; Clucas & Marzluff, 2012; Møller, 2008; Sprau & Dingemanse, 2017)

A different scenario may be represented by those 'synurbic' species (Francis & Chadwick, 2012) that have lived within human settlements for centuries. These species often show limited fear of humans and sometimes even directly exploit their association with food resources. As in the case of many populations dependent on carrion or garbage in traditional human societies which, often because of the ecosystem services they provide, do not persecute them e.g. (Gangoso et al., 2013). Information on the behavioural responses to humans by these urban specialists would complete our current picture of adaptation to a rapidly urbanising world and offer insights into the range of behavioural strategies potentially employed by urban wildlife to cope with a constant high proximity to humans (Evans et al., 2011; Kark et al., 2007).

One particularly interesting case of behavioural bottleneck (i.e. conflicting interests) faced by animals in urban environments is how to modulate their defence of young in a fixed nest or burrow against the potential danger presented by humans. Such modulation is especially relevant for large vertebrates armed with potentially dangerous weaponry and thus theoretically capable to drive humans away. This scenario is more complex than the one examined in studies of flight initiation distance, because the fitness investment at stake (the offspring) is not mobile and cannot be fully controlled by the animal (e.g. by fleeing). Thus, it may be particularly informative of the extent to which urban animals perceive humans as a threat, how much risk they are willing to take to defend their parental investment, and how this may vary along a range of urban configurations and human attitudes towards wildlife. To our knowledge, few studies have examined such aspects and most of them have focused essentially on the comparison of behavioural traits between urban and rural individuals (review in Lowry et al., 2013; Miranda et al., 2013). While this comparison renders important information on trait expression associated with the colonization of urban environments, it assumes that all individuals that colonized a city adopted the same behavioural strategies (Evans et al., 2011). However, urban environments are often highly heterogeneous mosaics with marked variation in physical structure or human density (Grimm et al., 2000; Lepczyk et al., 2017), to which animals are likely to respond, potentially selecting for a more complex array of behavioural strategies in urban animals than has thus far been recognized.

To explore these aspects, here we examine patterns of nest defense against humans by a synurbic raptor, the Black Kite *Milvus migrans*, which exploits humans for food in a megacity (Delhi, India) that incorporates a wide range of urban conditions, human densities and ritualized animal-feeding practices. The Black Kite (hereafter kite) is a medium-sized opportunistic

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raptor, widely distributed throughout Eurasia, Africa and Australia, and considered the most successful raptor in the world. In India, the native, resident subspecies M. m. govinda is synurbic (sensu Francis & Chadwick, 2012), occurring almost exclusively in close association with humans in towns and cities (Naoroji & Schmitt, 2007). In Delhi, kites breed on both trees and artificial structures (pylons, towers), sometimes forming loose colonies and locally reaching extremely high densities, thanks to the exploitation of human food 'subsidies' facilitated by inefficient refuse disposal and by religious kite-feeding practices (Kumar et al., 2014; Kumar et al., 2018); (see Study area below). In particular, the relationship between kites and humans in Delhi is dual: on one hand, kites depend on humans for food and thus over-select breeding sectors in the city close to ritual-feeding sites, and with a high density of humans and of their garbage in the streets (Kumar et al., 2018). On the other hand, people sometimes rob or destroy kite nests to collect nestlings for the illegal bird trade, or to remove dangerous nest materials from electricity pylons, telephone towers or light poles during maintenance operations (Kumar, 2013). Thus, humans approaching a nest can be perceived by kites as a potential threat to their offspring, soliciting a defense response.

We feel that this represents a particularly interesting case study because: (1) Delhi kites directly exploit association of humans with food, by accessing their waste or by grabbing meat offered to them by people through religious, ritual feeding practices. Thus, they frequently come into close contact with humans, which may affect their perception and fear of humans. (2) These offerings and garbage disposal practices vary dramatically through the city (see Study area below), implying that different kites may experience and perceive people in different ways through the urban mosaic. (3) As medium-sized raptors armed with sharp talons and high aerial agility, kites are potentially well capable to inflict injury on people and drive them away from

their nest-area. However, (4) much of the mortality experienced by kites, inflicted by external agents, is still of anthropogenic origin (Kumar, 2013), implying a delicate trade-off between the need to come close to humans for feeding but avoid them or repel them in the appropriate context to ensure their own or their offspring safety. Given all the above, when faced with people approaching their nest, kites will need to take a quick defense-tactic decision, which may reflect these conflicting pressures. Furthermore, the balance of these pressures may change through the complex mosaic offered by this megacity of 16 million people. In particular, because ready access to dense Muslim colonies, rich in ritual-subsidies, is considered a key resource in this population (see Kumar et al., 2014; Kumar et al., 2018 and Study area below), we hypothesized that it could alter the profitability for kites of hygiene levels, green cover or built-up cover, ultimately affecting the defense-value of the offspring.

3.2. Materials and Methods

This research is part of a larger and long-term study on the demography of Black Kites in Delhi and has received bioethical approval by the Training, Research, and Academic Council (TRAC) of the Wildlife Institute of India, Dehradun. The project took all precautions to ensure researcher and animal safety. The study did not involve human participants other than the research team.

Study area

Delhi is a megacity of more than 16 million inhabitants, currently covering an area of 1500 km² and in constant, rapid expansion (Census organization of India, 2011). It is polycentric and heterogeneous, with a multitude of juxtaposed urban configurations, which make it difficult to establish a linear urban-rural gradient. Two aspects of Delhi are important in determining the

food availability and habitat quality for kites (Kumar et al., 2018). First, large portions of the city are characterized by poor solid waste management, which affords food to kites in the form of carrion or refuse, and its associated prey-fauna (e.g. rodents, pigeons etc.). Secondly, many people (primarily in Muslim settlements) engage in the centuries-old religious practice of feeding meat scraps to kites (hereafter termed "ritualized-feeding") typically offered by throwing meat into the air for the birds to catch. These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries (Pinault, 2008; Taneja, 2015). Thus, waste management issues common to all communities, and cultural rituals which are more specific to some, generate spatial heterogeneity in the potential food availability for kites (Kumar et al., 2018).

Field procedures

We systematically surveyed kite nests during 2013–2016 at 24 plots of 1 km², which were randomly stratified within Delhi (1500 km²) so as to cover all its possible urban settings, from semi-natural to extremely built-up sites (details in Kumar et al., 2014). This resulted in a sample of 101 nests, each from a different territory, used at least once for breeding between 2013 and 2016. Nests were checked every 7–10 days until the chicks were at least 45 days old, in order to estimate the number of young raised to fledging (chicks fledge when about 48 days old) (see Kumar et al., 2014) for further details of nest checks and surveys). During each nest check, we assessed the intensity of offspring defense by the parents against our own human intrusion as follows. During each visit, a team consisting of a tree-climber (always the same for each nest) and one or two accompanying observers positioned themselves at a point from where the kite nest was in clear sight. The point was chosen so as to be clearly visible to the parent kite perched in the nest area. The team then walked slowly towards the nest. Once under the nest, we

observed the behaviour of the adults for 20 minutes while the tree-climber reached the nest and checked its content. We classified the intensity of defense according to the following ordinal score: (score 0) the kite remains perched at a distance (> 20 m) or flies far away, either silently or after alarm-calling a few times; (score 1) it flies directly above the field-team in an excited manner while calling repeatedly, or perches close-by (within 20 m) and alarms continuously, or perches within a few metres of the climber (within the same nesting tree); and (score 2) it repeatedly dive-bombs at the climber and ground-team, it may even stoop among tree-branches or electricity wires, or perch a few metres from a team-member and then stop again, sometimes hitting or scratching with open talons, while continuously alarm-calling (See supplementary resource). Thus, progressively higher scores were associated with higher costs and risks for the defending kite, including (a) increase in energy costly activities, such as alarm-calling or flapping flight, and (b) increase in potential risks, such as injuries while maneuvering through the canopy or overhead electric wires. Throughout, the defense score refers to the maximum intensity of defense shown by either of the partners of each pair. This was justified by the fact that: (1) kites are monomorphic, making it impossible to distinguish males from females; and (2) no major difference in defense levels was noticed between the two partners of a pair (if one attacked, the other also attacked, while if one remained quietly perched, the other did the same). All defense ratings were carried out between 08:00 and 18:00 hrs (local time) avoiding unusual weather conditions (e.g. rain, or excessive heat).

Predictors of offspring defense

To investigate how kite defense varied across the Delhi mosaic of urban structure, human densities and practices, we measured a series of environmental, urban and human variables previously found to be important components of habitat quality and food availability in this population (Kumar et al., 2018). These variables are detailed in Table 1 and were devised so as to characterise: (1) the timing, context and characteristics of the defense trial (e.g. number of people in the visiting team, number of previous visits to a target nest); (2) the breeding stage, social setting (intraspecific spacing) and content of the nest during the trial (e.g. number of offspring to be defended); (3) the physical features of the nest and its immediate surroundings (e.g. its location within a hedge, park or continuous woodland); (4) the urban landscape structure around the nest (e.g. local road density or extent of impervious surfaces in the surroundings); and (5) direct and indirect estimates of human activities and practices (e.g. access to dense Muslim colonies for reasons stated above, efficiency of waste management, or human density). Further details of the recorded variables and their ecological rationale are given in Table 1 and in (Kumar et al., 2018)

Table 1 Variables measured during nest defense trials conducted at Black kite nests within the city of Delhi (India)

Variable	Description, rationale for use and predicted effect
Julian date	Julian date of nest inspection. Earlier laying raptors are often older or higher quality individuals with higher parental investments and were thus expected to be more aggressive (Newton, 1979).
Breeding stage	The breeding cycle was divided into five main stages: (1) pre- incubation; (2) incubation (3) nestlings younger than 15 days; (4) nestlings of 15 - 30 days; (5) pre-fledging: 30 - 48 days old nestlings; (6) post-fledging. We expected defense to vary by stage because avian nest defense often varies through the breeding season in conjunction with the growing survival probabilities of the offspring e.g. (Hakkarainen, & Korpimäki, 1994; R Development Core Team, 2009; Sergio & Bogliani, 2001).
Previous visits	Number of previous nest checks by the research team. This variable was fitted to control for potential habituation or reinforcement of aggressiveness by repeated sampling of the same pair (Newton, 1979).
Team size	Number of people in the research team (2 or 3). This was fitted to examine the impact of the number of intruders on defense, if any.
Number of onlookers	Number of people (not belonging to the field-team) within 20 m of the nest during the defense trial. This was fitted to examine the impact of the number of onlookers on defense, if any.
Number of offspring	Number of eggs or chicks in the nest at the time of the defense trial. We expected higher aggression by pairs with larger parental investments, as found in some previous studies e.g. (Hakkarainen, & Korpimäki, 1994; R Development Core Team, 2009; Sergio & Bogliani, 2001).
NND5 (m)	Mean distance to the five closest kite neighbors. This variable focused on the impact of local, spatial arrangement on defense intensity. We expected higher defense under more crowded conditions (i.e. at higher quality, more attractive sites, which may entail higher parental investments).

Territories within 200 m	Number of territories occupied within 200 m of the target nest. This variable focused on the impact of local density on defense intensity. We expected higher defense levels at higher local densities (i.e. at higher quality, more attractive sites, which may entail higher parental investments).
Colony size	Number of nests within the kite colony. We expected larger colonies to be more attractive to individuals of a semi-social species, or to be associated with higher vigilance and larger food supplies, leading to a higher motivation for defense.
Tree arrangement	Categorical variable: $1 = \text{isolated tree/pylon}$; $2 = \text{line of trees (e.g. along an avenue}$); $3 = \text{parkland (scattered trees with > 5-10 m of open ground between them, typically grassland in urban parks)}$; $4 = \text{woodlot}$. These habitat configurations are known to be differentially attractive to Delhi kites (Kumar et al., 2018) and were fitted in order to investigate links between habitat quality, urban landscape configuration and defense intensity.
Balcony	Categorical variable: 0 = absence, 1 = presence of a balcony within 20 m of the nest. We predicted that pairs in such close and constant contact with humans could show higher aggressiveness through habituation and loss of fear.
Index of road density	Number of asphalted roads crossed by a 500 m north-south and a 500 m east-west transect crossing each other on the nest. Delhi kites over-select areas with more extensive road networks, which are one of their main foraging habitats (Kumar et al., 2018). Thus, we expected defense-levels to increase with road density.
Urban cover	Percentage area covered by built-up structures (buildings, roads, parking lots, or any other impervious surface) within 500 m of the nest. Urban and tree cover were fitted to investigate links between offspring defense and urban landscape configurations. Urban cover was also fitted as a quadratic effect to test the "intermediate disturbance hypothesis" commonly proposed in the urban ecology literature (Shea, 2004), by which the favorability of urban ecosystems to wildlife peaks at intermediate levels of the urbanization gradient.
Green cover	Percentage area covered by shrub/tree vegetation within 500 m of the nest. Urban and tree cover were fitted to investigate links between offspring defense and urban landscape configurations.

- Hygiene score Level of sanitation: 1 = clean areas; 2 = areas under poor waste management regimes •. The level of street sanitation is an important component of habitat quality for this population (Kumar et al., 2018). We expected higher aggression at sites with lower sanitation because of frequent exposure to humans and because larger food supplies may imply larger broods and thus higher parental investments.
- Human density Average number of people walking within 2m of a stationary observer during 5 min at 10 locations randomly plotted within 200 m of the nest ^b. Delhi kites over-select sites with intense human activity in the streets, leading to more food in the form of human refuse (Kumar et al., 2018). We expected defense-levels to increase with human density in the streets because of frequent exposure to humans and because larger food supplies may imply larger broods and thus higher parental investments.

Access to First component (PC1) of a principal component analysis on Muslim density and on the proximity to the three Closest Muslim colonies (see Methods). Muslim subsidies are one of the main food resources for Delhi kites (Kumar et al., 2018; Kumar et al., 2014) and ready access to them was predicted to boost offspring-defense because of frequent exposure to humans and because larger food supplies may imply larger broods and thus higher parental investments.

[•] Categorical variable with two levels: 1 = efficient waste disposal with very scarce or no organic refuse in the streets; 2 = abundant and widespread refuse in the streets throughout the area, either in small frequent piles, in illegal ephemeral dumps, or as individual items scattered a bit of everywhere through all streets (Kumar et al., 2018).

^{*} Counts were only operated between 10:00-17:00 hrs and avoided during atypical, momentary peak periods of human traffic, such as exits from work or schools, in order to maintain consistency across sites

In particular, a key variable in our previous analyses on the predictors of kite site selection, occupancy and breeding performance was the ease of access to dense Muslim colonies, which provide abundant food supplies in the form of ritual subsidies (Kumar et al., 2018). More specifically, we previously showed that Delhi kites over-selected for breeding sites closer than available to the 1st, 2nd and, possibly, 3rd nearest Muslim colony (see Kumar et al., 2018 for details). Thus, to provide a comprehensive measure that integrated the proximity to the three nearest Muslim colonies with their human population density (under the assumption that higher rates of refuse and ritualized-feeding should occur in more densely-populated Muslim colonies), we extracted the first component of a PCA (Tabachnick & Fidell, 1996) run on these four aforementioned variables. Its PC1 (hereafter "access to Muslim subsidies") explained 65% of the variance and had a high positive loading on Muslim population density and high negative loadings on the distance to the 1st, 2nd and 3rd closest Muslim colonies. Thus, it provided an increasing index of access to abundant "Muslim subsidies".

Statistical analysis

We employed a linear mixed effect ordinal regression (cumulative-link mixed effect model), (Agresti, 2010; Hedeker & Gibbons, 1994) through package "ordinal" (Christensen, 2018) to examine the effect of environmental, urban and human variables on the ordinal score of offspring defense. The ordinal regression was run on 657 defence trials conducted at 101 unique nesting territories. Because territories were sampled repeatedly, and because territories within the same plot were closer and thus potentially more similar than territories sampled in different plots, we fitted as a random effect territory identity nested within plot identity and year, so as

to control for pseudoreplication and spatial autocorrelation (Zuur et al., 2009). To reduce collinearity and the number of variables presented to the logistic regression, we considered pairs of strongly inter-correlated variables (r > 0.60) as estimates of a single underlying factor, and only retained for analysis the one estimated to be more biologically important for the study organism.

To explore further the potential link between defense intensity and subsequent breeding benefits, we related the eventual number of fledged young to the intensity of defense during incubation (i.e. about two months before fledging) by means of a linear mixed model, again with territory identity nested within plot identity and year as a random term.

All multivariate models were built through a backward stepwise procedure following Zuur et al., 2009, all explanatory variables were fitted to a maximal model, extracted one at a time from the maximal model, and the associated change in model deviance was assessed by the significance of a likelihood-ratio test; the procedure was repeated until we obtained a final model which only included significant variables (Zuur et al., 2009). To avoid overparameterization, we ensured never to fit more than N/3 variables to each maximal model, where N is the sample size of the analysed dataset (Crawley, 2012). Interactions were fitted only when we had a priori hypotheses about their potential effect, based on our field observations and knowledge of the population. To explore the possibility of curvilinear relationships, we fitted continuous variables as linear and also as quadratic terms. Explanatory variables were fitted as standardized Z-scores because of their different measurement units and in order to better evaluate their relative importance (Grueber et al., 2011). Model assumptions were checked by investigating QQ plots, histograms of residuals, and plots of standardized and normalized residuals against fitted values and against explanatory variables (Zuur et al., 2009; Crawley, 2012). All mixed models were implemented in R.3.4.3 (R Development Core Team, 2009), all tests are two-tailed, statistical significance was set at < 0.05, and all means are given ± 1 SE.

3.3. Results

Several variables entered the mixed model ordinal regression (Table 2). First, defense intensity increased progressively along the breeding cycle and then declined in its final stages, especially after the young fledged from the nest (Fig. 1a). Second, defense levels increased with the number of offspring in the nest (Fig. 1b). Third, the interaction of Access to Muslim subsidies and Hygiene score was also significant (Table 2 and Fig. 1c): under conditions of poor sanitation, defense levels increased more steeply with access to dense Muslim colonies than under cleaner conditions, suggesting that low sanitation and ready access to Muslim subsidies acted in concert, i.e. synergistically affecting aggressiveness. Fourth, defense intensity declined with the green cover and was minimum at intermediate levels of built-up cover (Table 2a).

Finally, the number of fledglings produced by a pair was positively related to the defense intensity recorded for the same pair about two months earlier during incubation (Table 2b and Fig.2).

Table 2 Cumulative-link mixed effect ordinal regression (a) testing the effect of environmental, urban and human variables on the ordinal intensity of offspring defense; and (b) linear mixed effect model testing the effect of intensity of offspring defense in incubation on eventual fledgling production

Variable		$\beta \pm SE$	Z-test	<i>P</i> - value
a.	Dependent variable: Intensity of defense (N = 657) ^{a,b}			
	Breeding Stage (incubation)	1.11 ± 0.8	1.39	0.164
	Breeding Stage (small nestling)	3.11 ± 0.82	3.81	< 0.001
	Breeding Stage (large nestling)	3.83 ± 0.8	4.78	< 0.0001
	Breeding Stage (pre-fledging)	2.34 ± 0.76	3.07	0.002
	Breeding Stage (post-fledging)	0.71 ± 0.97	0.73	0.463
	Offspring number	1.61 ± 0.33	4.81	< 0.0001
	Access to Muslim subsidies	-6.23 ± 2.01	-3.1	0.001
	Hygiene score	3.25 ± 1.01	3.24	0.001
	Access to Muslim subsidies * Hygiene score	4.5 ± 2.02	2.22	0.026
	Green cover	-1.65 ± 0.68	-2.4	0.016
	Urban cover	-3.69 ± 1.62	-2.28	0.022
	Urban cover ^2	3.20 ± 1.67	1.9	0.057
b.	Dependent variable: fledglings produced ^c (N			
	= 103)			
	Intensity of defense (during incubation)	0.28 ± 0.12	2.27	0.023
	Intercept	-0.36 ± 0.17	-	-

^a Cumulative link mixed model with a logit link function, based on N = 657 defense trials from 101 independent territories. The dependent variable is the ordinal score of offspring defense intensity. Territory-identity nested within plot-identity and year was fitted as a random factor.

^b Variables presented to the model: Julian date, Team size, Number of onlookers, Previous visits, Breeding Stage, Offspring number, NND5, Territories within 200 m, Tree arrangement, Balcony, Index of road density, Urban cover, Green cover, Hygiene score, Human density, Access to Muslim subsidies, Access to Muslim subsidies*Hygiene score, Access to Muslim subsidies*Urban cover, Access to Muslim subsidies*Green cover (the rationale for fitting interactions can be found in the Methods).

^c Generalised linear mixed model with Poisson errors and a logit link function, based on N = 103 defense trials from 60 independent territories sampled during incubation. The dependent variable is the number of young raised to fledging stage. Territory-identity nested within plot-identity and year was fitted as a random factor.


a

b

Fig 1. The intensity of offspring defense by kites in Delhi (India) varied with: panel (a) the stage of the breeding cycle; and panel (b) the number of offspring (eggs and/or chicks) in the nest at the time of the defense trial. Error bars represent ± 1 SE.



С

Fig. 1c. The intensity of offspring defense by kites in Delhi (India) varied with: panel (c) the interaction between access to Muslim subsidies and the amount of human waste in the streets (the black circles and the solid line indicate breeding sites with poor street sanitation, while the white quadrats and dotted line portray cleaner sites with less refuse in the streets). In panel c, Access to Muslim subsidies is shown above and below the median value ("high" and "low", respectively) for clarity of presentation. Error bars represent ± 1 SE.



Fig. 2. Number of fledglings produced by a pair in relation to the defense intensity exhibited by that pair two months earlier during incubation. Error bars represent ± 1 SE.

4.4. Discussion

Kite defense levels progressively increased through the breeding cycle and reflected the number of offspring in the nest during each trial. These results confirmed those of several earlier studies e.g. (Hakkarainen & Korpimäki, 1994; Møller & Nielsen, 2014; Sergio & Bogliani, 2001) and suggested that parents tuned their defense response in relation to their parental investment, i.e. on the quantity and future survival prospects of their offspring, which increased through the breeding cycle. The fact that defense intensity early in the season predicted eventual young production months later, by the end of breeding, implied three non-exclusive possibilities: (1) parents could estimate the eventual likelihood of breeding success early in the season and set their defense accordingly; (2) aggressive nest defense lowered predation rates at the nest, with consequent benefits for young production; or (3) high quality individuals (e.g. healthier, or larger) were simultaneously more aggressive and better breeders, generating a positive association between two parameters separated by months in time. For example, kites that were more aggressive against humans could potentially be more aggressive against other more common nest predators such as crows or monkeys (Kumar et al., 2014). In support of this idea, in another study, nest defense by a falcon was experimentally shown to lower nest predation rates by corvids (Sergio & Bogliani, 2001). The above mix of associative and causative mechanisms produced results that are typical of avian nest defense studies e.g. (Montgomerie & Weatherhead, 1988; Redondo, 1989), suggesting that life in an urban setting did not disrupt the typical links between behavioural traits and vital rates found in avian populations.

More notably, despite constant close exposure to people, kite defense suggested that humans were not perceived as a neutral component of the urban landscape, but rather as a potential danger when they approached a nest. This implied a capability by kites to discriminate human attitudes and adjust their behaviour in a context-dependent manner, approaching people to very close quarters for feeding but fleeing and sometimes even attacking them when defending their offspring. Furthermore, defense levels varied through the city in relation to cultural ritual-feeding practices, refuse management and landscape composition. In particular, defense intensity was higher at sites that combined ready access to dense Muslim colonies (where kites are fed by humans by tossing meat-scraps at very close quarters) with poor sanitation (which promotes frequent feeding on anthropogenic waste close to people, e.g. at ephemeral garbage dumps also used by poor rag pickers digging for useful materials). This spatial association could be the result of three non-exclusive mechanisms: (a) frequent and reiterated, close contact with humans may have lowered fear, thus enhancing boldness and aggression; (b) sites close to ritual-feeding areas or with poor sanitation are over-selected by kites and thus likely occupied by higher quality individuals with higher parental investments (Kumar et al., 2018), leading to higher defense intensity; and (c) bolder individuals may be more likely to withstand constant close proximity to humans and a bolder temperament is associated with greater aggression in some species e.g. (Evans et al., 2010). Thus, individual quality, personality, habituation and motivation may have generated a spatial association between a behavioural strategy and a human cultural landscape, thus contributing to the growing appreciation of the importance of human cultural geographies for urban ecology e.g. (Alberti, 2008; Forman, 2014; Lepczyk et al., 2002; Pickett et al., 2016)

While the exact mechanism remains uncertain, the behavioural response of kites to a perceived threat was finely tuned on the spatial arrangement of human activities and ritual practices, their consequent attitudes towards the birds, and their waste management organization. In turn, this would create a dynamic behavioural landscape, reflecting the

underlying urban mosaic of resources, structures and human attitudes, to which kites will necessarily have to adapt and respond, as shown for species that colonized urban environments more recently (Evans et al., 2010).

The fact that aggression peaked at close human proximity suggested that close coexistence and habituation to people led to a loss of fear and heightened boldness towards humans, rather than an enhanced capability to avoid them by keeping a "low profile" or learning to ignore them. Such dynamics may have been further favoured by the generally positive, religiously-based attitudes of Indian people towards wildlife, as reported by several studies e.g. (Bagchi & Mishra, 2006; Karanth et al., 2013; Saberwal, 2001)

Overall, these results confirm and extend earlier findings of more aggressive offspring defense by urban than rural individuals of a given species e.g. (Knight et al., 1987; Kunca & Yosef, 2016; Moroni et al., 2017), suggesting that the route to close coexistence with humans is often accompanied by fine-grained, context-dependent strategies and trade-offs, rather than evolution of "blind tolerance" and indifference towards human activities (Dingemanse et al., 2010). In this sense, most animals making frequent contact with humans (through colonization of urban habitats, or through peri-urban encroachment) will likely need to develop cognitive capabilities and behavioural tactics that will enable them to exploit humans and cope with their omnipresent disturbance rather than learning to ignore them, in order to attain long-term coexistence e.g. (Carrete & Tella, 2011; Vincze, 2016). In turn, acquisition of such traits will likely be shaped by a two-way interaction between human perceptions, attitudes and practices on one part and daily experience and habituation to humans on the part of the animal. For synurbic species, like kites, at the high end of the spectrum of adaptation to an urban life, the above cited interaction may lead to behavioural and demographic traits fine-tuned not only on

urban physical structures, but also on human cultural practices and attitudes, which for many species may become the most important, defining dimensions of their urban niche.

To date, most studies of animal behavioural responses to urbanization have focused on the comparison between urban and rural individuals, in order to draw inferences on the characteristics that enable or mediate the colonization of highly anthropogenic urban environments e.g. (Carrete & Tella, 2011; Lowry et al., 2013; Møller, 2008). Here, we show that marked heterogeneity in behavioural responses to humans also continue to exist within cities and after centuries of initial urban colonization, suggesting further fine-tuning of behavioural traits on specific dimensions of the urban environment. In this sense, the urbanrural comparison does not target the end-result of colonization, but rather defines only the beginning of a hierarchical process of adaptation to humans, who are increasingly concentrated in cities. Thus, more research is needed on the fine-grained adjustments to urban structure and human culture by animals that are already in their mature stage of adaptation to an urban life.

Acknowledgments

We are grateful to Ben Sheldon, Chris Perrins, Tommaso Pizzari, Ujjwal Kumar, and the Director, Dean and research coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. We thank Drs. A. Margalida, W. Cresswell and two anonymous reviewers for helping us to improve a first draft of the manuscript. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Delhi Transport Corporation, Civic bodies of the Government of NCT of Delhi helped with legal permits, and the Director of the National Zoological Park of New Delhi gave access to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We express our most heartfelt gratitude to all the volunteers of the "Black Kite Project Group" from the University of Delhi (Sri Venkateswara and Deshbandhu Colleges), especially U. Gupta, H. Malhotra, A. Singh, P. Kumar, H. Singh, U. Nair and M. Singh, who provided essential field help, enthusiasm and cooperation in the environmental education of locally assembling crowds of curious people. Special thanks to our field assistants Laxmi Narayan, Prince Kumar and Poonam, who were the backbone of the field team. Finally, thanks to all the landowners, managers and government officials who patiently cooperated with our constant requests of access. We are thankful to the Publication Fee Assistance for financial support towards the publication of this manuscript.

References

- Agresti, A. (2010). Analysis of ordinal categorical data (Vol. 656). John Wiley & Sons.
- Alberti, M. (2008). Advances in urban ecology: integrating humans and ecological processes in urban ecosystems (No. 574.5268 A4). New York: Springer.
- Bagchi, S., & Mishra, C. (2006). Living with large carnivores: predation on livestock by the snow leopard (Uncia uncia). *Journal of zoology*, *268*(3), 217-224.
- Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal behaviour*, *71*(2), 389-399.
- Carrete, M., & Tella, J. L. (2011). Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PloS one*, *6*(4), e18859.
- Census Organisation of India. (2011). Office of the Registrar General & Census Commissioner, India <u>http://censusindia.gov.in/2011census</u>
- Chamberlain, D. E., Cannon, A. R., Toms, M. P., Leech, D. I., Hatchwell, B. J., & Gaston, K. J. (2009). Avian productivity in urban landscapes: a review and meta- analysis. *Ibis*, 151(1), 1-18.
- Christensen, R. H. B. Regression Models for Ordinal Data [R package ordinal version 2018.4-19].
- Clucas, B., & Marzluff, J. M. (2012). Attitudes and actions toward birds in urban areas: human cultural differences influence bird behavior. *The Auk*, *129*(1), 8-16.
- Crawley, M. J. (2012). The R book. John Wiley & Sons.
- Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in ecology & evolution*, 25(2), 81-89.
- Evans, J., Boudreau, K., & Hyman, J. (2010). Behavioural syndromes in urban and rural populations of song sparrows. *Ethology*, *116*(7), 588-595.

- Evans, K. L., Hatchwell, B. J., Parnell, M., & Gaston, K. J. (2010). A conceptual framework for the colonisation of urban areas: the blackbird Turdus merula as a case study. *Biological Reviews*, 85(3), 643-667.
- Evans, K. L., Chamberlain, D. E., Hatchwell, B. J., Gregory, R. D., & Gaston, K. J. (2011). What makes an urban bird?. *Global Change Biology*, *17*(1), 32-44.
- Forman, R. T. (2014). Urban ecology: science of cities. Cambridge University Press.
- Francis, R. A., & Chadwick, M. A. (2012). What makes a species synurbic? *Applied Geography*, 32(2), 514–521.
- Gangoso, L., Agudo, R., Anadón, J. D., de la Riva, M., Suleyman, A. S., Porter, R., & Donázar, J. A. (2013). Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem services providers. *Conservation Letters*, 6(3), 172-179.
- Grimm, N. B., Grove, J. G., Pickett, S. T., & Redman, C. L. (2000). Integrated approaches to long-term studies of urban ecological systems: Urban ecological systems present multiple challenges to ecologists—Pervasive human impact and extreme heterogeneity of cities, and the need to integrate social and ecological approaches, concepts, and theory. *AIBS Bulletin*, 50(7), 571-584.
- Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *Journal of evolutionary biology*, 24(4), 699-711.
- Hahs, A. K., & Evans, K. L. (2015). Expanding fundamental ecological knowledge by studying urban ecosystems. *Functional Ecology*, *29*(7), 863-867.
- Hakkarainen, H., & Korpimäki, E. (1994). Nest defence of Tengmalm's owls reflects offspring survival prospects under fluctuating food conditions. *Animal Behaviour*, 48(4), 843-849.
- Hedeker, D., & Gibbons, R. D. (1994). A random-effects ordinal regression model for multilevel analysis. *Biometrics*, 933-944.
- Karanth, K. K., Naughton-Treves, L., DeFries, R., & Gopalaswamy, A. M. (2013). Living with wildlife and mitigating conflicts around three Indian protected areas. *Environmental management*, 52(6), 1320-1332.

- Kark, S., Iwaniuk, A., Schalimtzek, A., & Banker, E. (2007). Living in the city: can anyone become an 'urban exploiter'?. *Journal of Biogeography*, *34*(4), 638-651.
- Knight, R. L., & Temple, S. A. (1986). Why does intensity of avian nest defense increase during the nesting cycle?. *The Auk*, 318-327.
- Knight, R. L., Grout, D. J., & Temple, S. A. (1987). Nest-defense behavior of the American crow in urban and rural areas. *The condor*, *89*(1), 175-177.
- Kumar N. (2013) A study of resource selection by Black Kites *Milvus migrans* in the National Capital Region. M.Sc. Thesis submitted to Wildlife Institute of India; Saurashtra University. Rajkot. Gujarat
- Kumar, N., Mohan, D., Jhala, Y. V., Qureshi, Q., & Sergio, F. (2014). Density, laying date, breeding success and diet of Black Kites Milvus migrans govinda in the city of Delhi (India). *Bird study*, 61(1), 1-8.
- Kumar, N., Gupta, U., Jhala, Y. V., Qureshi, Q., Gosler, A. G., & Sergio, F. (2018). Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools. *Urban Ecosystems*, 21(2), 339-349.
- Kunca, T., & Yosef, R. (2016). Differential nest-defense to perceived danger in urban and rural areas by female Eurasian sparrowhawk (Accipiter nisus). *PeerJ*, *4*, e2070.
- Lepczyk, C. A., Warren, P. S., Machabée, L., Kinzig, A. P., & Mertig, A. G. (2012). Who feeds the birds. *Stud Avian Biol*, 45, 267-284.
- Lepczyk, C. A., Aronson, M. F., Evans, K. L., Goddard, M. A., Lerman, S. B., & MacIvor, J. S. (2017). Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. *BioScience*, 67(9), 799-807.
- Lowry, H., Lill, A., & Wong, B. B. (2013). Behavioural responses of wildlife to urban environments. *Biological reviews*, 88(3), 537-549.
- McDonnell, M. J., & Hahs, A. K. (2015). Adaptation and adaptedness of organisms to urban environments. *Annual review of ecology, evolution, and systematics*, *46*, 261-280.
- Miranda, A. C., Schielzeth, H., Sonntag, T., & Partecke, J. (2013). Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity?. *Global Change Biology*, *19*(9), 2634-2644.

- Montgomerie, R. D., & Weatherhead, P. J. (1988). Risks and rewards of nest defence by parent birds. The Quarterly Review of Biology, 63(2), 167-187.
- Moroni, E., Crivelaro, A. Z., Soares, T. L., & Guillermo- Ferreira, R. (2017). Increased behavioural responses to human disturbance in breeding Burrowing Owls Athene cunicularia. *Ibis*, 159(4), 854-859.
- Møller, A. P. (2008). Flight distance of urban birds, predation, and selection for urban life. *Behavioral Ecology and Sociobiology*, *63*(1), 63.
- Møller, A. P., & Nielsen, J. T. (2014). Parental defense of offspring and life history of a longlived raptor. *Behavioral Ecology*, 25(6), 1505-1512.
- Naoroji, R., & Schmitt, N. J. (2007). *Birds of prey of the Indian subcontinent*. Om Books International.
- Newton I. (1979). Population ecology of raptors. Poyser, Berkhamstead, UK.
- Pickett, S. T., Cadenasso, M. L., Childers, D. L., McDonnell, M. J., & Zhou, W. (2016). Evolution and future of urban ecological science: ecology in, of, and for the city. *Ecosystem Health and Sustainability*, 2(7), e01229.
- Pinault, D. (2008). Raw meat skyward: pariah-kite rituals in Lahore. *Equinox Publishing*, 108-121.
- R Development Core Team [Internet]. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL; c2009 [cited 27 Sept 2018]. Available from: <u>http://www.R-project.org</u>
- Redondo, T. (1989). Avian nest defence: theoretical models and evidence. *Behaviour*, 111(1), 161-195.
- Saberwal, V. K. (2001). *People, parks, and wildlife: Towards coexistence* (Vol. 14). Orient Blackswan.
- Sergio, F., & Bogliani, G. (2001). Nest defense as parental care in the northern hobby (Falco subbuteo). *The Auk*, *118*(4), 1047-1052.

- Shea, K., Roxburgh, S. H., & Rauschert, E. S. (2004). Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology letters*, 7(6), 491-508
- Smart, J., Amar, A., Sim, I. M., Etheridge, B., Cameron, D., Christie, G., & Wilson, J. D. (2010). Illegal killing slows population recovery of a re-introduced raptor of high conservation concern–the red kite Milvus milvus. *Biological Conservation*, 143(5), 1278-1286.
- Sprau, P., & Dingemanse, N. J. (2017). An approach to distinguish between plasticity and nonrandom distributions of behavioral types along urban gradients in a wild passerine bird. *Frontiers in Ecology and Evolution*, 5, 92.
- Tabachnick, B. G., & Fidell, L. S. (1996). Using Multivariate Statistics. Harper Collins. New York.
- Taneja, A. V. (2015). Saintly animals: the shifting moral and ecological landscapes of North India. *Comparative Studies of South Asia, Africa and the Middle East*, *35*(2), 204-221.
- Vincze, E., Papp, S., Preiszner, B., Seress, G., Bókony, V., & Liker, A. (2016). Habituation to human disturbance is faster in urban than rural house sparrows. *Behavioral Ecology*, 27(5), 1304-1313.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). GLM and GAM for count data. In *Mixed effects models and extensions in ecology with R* (pp. 209-243). Springer, New York, NY.

Human-attacks by an urban raptor are tied to human subsidies and religious practices

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Accepted for publication on December 27, 2018; in press, Scientific Reports.

• <u>Uncorrected Proof typesetting included in the Appendix</u>



Abstract

Growing urbanization is increasing human-wildlife interactions, including attacks towards humans by vertebrate predators, an aspect that has received extremely scarce investigation. Here, we examined the ecological, landscape and human factors that may promote humanaggression by raptorial Black kites *Milvus migrans* in the 16-millions inhabitants' megacity of Delhi (India). Physical attacks depended on human activities such as unhygienic waste management, ritual-feeding of kites (mainly operated by Muslims), human density, and presence of a balcony near the nest, suggesting an association between aggression and frequentclose exposure to humans and derived food-rewards. Surprisingly, while more than 100,000 people could be at risk of attack in any given moment, attitudes by local inhabitants were strikingly sympathetic towards the birds, even by injured persons, likely as a result of religious empathy. These results highlight the importance of socio-cultural factors for urban biota and how these may radically differentiate the under-studied cities of developing countries from those of western nations, thus broadening our picture of human-wildlife interactions in urban environments. The rapid sprawling of urban and suburban areas with their associated foodsubsidies is likely to increase proximity and exposure of large predators to humans, and vice versa, leading to heightened worldwide conflicts.

Keywords: ethnozoology; human-wildlife conflict; mitigation; raptors; urban management

4.1. Introduction

There is growing interest in the interactions between human culture and animals, as evidenced by the rapid spread of studies in the field of ethnozoology (Alves, 2012; Alves & Albuquerque, 2018; Tidemann & Gosler, 2012). The need for integration of human socioeconomic and cultural variables into ecological research is particularly obvious in studies that focus directly on humanwildlife conflicts, or on expanding anthropogenic environments such as cities, where urban residents are confronted with a "novel" human-wildlife interface (Alberti, 2008; Dickman, 2010; Redpath et al., 2013; Torres et al., 2018)

In particular, worldwide urban residents are experiencing a growing frequency of encounters with wildlife due to increasing urbanization, human encroachment of natural habitats, occasional expansion of green-spaces within cities, intentional feeding to attract wildlife, and growing adaptation of animal species to urban ecosystems (Gaston et al., 2010; Marzluff et al., 2008; Soulsbury & White, 2015). While close encounters may be beneficial in reconnecting urban people with 'nature' (Cox & Gaston, 2016; Hosey & Melfi, 2014), such increasing contacts are accompanied by an equally growing rate of human-wildlife conflicts, such as vehicle collisions, property damage, pet predation, disease transmission and even physical attacks on humans (Conover, 2001; Cypher, 2013; Hadidian, 2015). Conflicts of this kind are typically difficult to manage because socio-political and cultural attitudes and perceptions often make mitigation controversial (Dickman, 2010; Messmer, 2000). This is especially pronounced in urban settings, which may pool together people with very different cultural backgrounds and with substantial differences in their interest or tolerance of wildlife, let alone of nuisance animals (Bjerke & Østdahl, 2004; Conover, 1997; Hadidian, 2015) Furthermore, urban animals may behave differently from their rural counterparts, thus requiring specially-designed mitigation measures.(Ditchkoff et al., 2006)

An extreme and sometimes dramatic form of human-wildlife conflict is represented by direct physical attacks on humans, which may cause psychological distress, diseases, injuries, sometimes severe or permanent ones, and even loss of life (Jones & Thomas, 1999; Kofron, 1999; Kushnir et al., 2010; Sudarshan, 2007; Torres et al., 2018). Similar to other forms of conflict, the frequency and severity of aggression on humans seem to be increasing in many urban areas (Bhatia et al., 2013; Siemer et al., 2009; Thornton & Quinn, 2009; Timm, 2004). This creates an urgent need to know the potential drivers and risk factors underpinning the attacks, in order to devise mitigation strategies and avoid conflict, which might prejudice peoples' perceptions and actions towards wildlife in general (Dickman et al., 2014; Hazzah et al., 2017; St. John et al., 2011)

A special subset of these potentially-aggressive species is represented by vertebrate top predators, such as mammalian carnivores or birds of prey. Because of their armament, harm potential, and dangerous iconic nature in collective imagery, these species typically evoke more emotional responses and intolerance than other species (Elliot et al., 2016; Fascione et al., 2004; Gehrt et al., 2010), frequently leading to "hyper-perception of risk" (Dickman, 2010) For example, Kellert (1980) showed that people tend to be more afraid of species that have the potential to harm them. Independently of perceptions, some of these predators have colonized many cities and increased dramatically in some urban areas in recent decades, sometimes reaching densities unparalleled in rural areas (Bateman & Fleming, 2012; Bird et al., 1996; Gehrt et al., 2010; Rutz, 2008; Timm, 2004). In turn, this has increased encounters and conflict, sometimes with well demonstrated upturns in attack rates and even fatalities, frequently sensationalized by the public media (Bhatia et al., 2013; Thornton & Quinn, 2009; Timm, 2004; Siemer et al., 2009). In many cases, increased aggression has been linked with intentional and

unintentional human feeding of the predators, resulting in consequent loss of fear (Bounds & Shaw, 1994; McCullough, 1982; Thompson et al., 2003). Despite all the above, very few studies have examined the conditions that may predispose certain individuals to attack humans, and most of them have focused on mammals in rural areas (Hockings et al., 2010; Kushnir et al., 2014; Nyhus & Tilson, 2004; Torres et al., 2018) Thus, there is a great need for information from urban areas and other taxonomic groups to advance knowledge in this field. Here we assess the ecological, landscape and human factors that may promote aggression towards humans by raptorial Black Kites *Milvus migrans* (Fig. 1) in Delhi (India), a megacity of 16-million inhabitants, which hosts one of the largest concentrations of vertebrate predators of the world (Kumar et al., 2014). In particular, we tested the hypothesis that individuals more exposed to human feeding and subsidies may be more likely to attack humans.

The Black Kite (hereafter "kite") is a medium-sized, opportunistic predator and facultative scavenger. It is considered the most successful raptor in the world, due to its capability to withstand anthropogenic habitat change and even breed in high numbers alongside dense human populations within cities, especially in tropical areas (Ferguson-Lees & Christie, 2001). Throughout its distribution, there are reports of individuals snatching food from humans, sometimes in aggressive ways, up to the point of being considered a local nuisance (Galbreath et al., 2014; Parker, 1999). In India, the native, resident subspecies *M. m. govinda* is synurbic (Francis & Chadwick, 2012), i.e. it occurs almost exclusively in close association with humans in towns and cities (Naoroji, 2006). In Delhi, where this study was conducted, kites breed throughout the city, often a few meters from human habitation, and locally reach extremely high densities, thanks to the exploitation of human food subsidies facilitated by inefficient refuse disposal and by religious kite-feeding practices (Kumar et al., 2014; Kumar et al., 2018). These

centuries-old religious offerings (hereafter termed 'ritualized-feeding') consist in throwing meat scraps into the air for the kites to catch and are made for a variety of reasons, such as asking for blessings and relief from sins and worries (Pinault, 2008; Taneja, 2015). Whilst meat-offering is practiced by a number of communities, in Delhi it is especially prevalent amongst members of Islamic faith, whose numbers are concentrated in well-defined portions of the city (hereafter 'Muslim colonies') where large quantities of meat are tossed to kites at predictable hours each day, sometimes causing hundreds of kites to congregate. Breeding individuals of this kite population often dive-bomb, scratch and harm humans with their talons when these approach their nest, sometimes causing deep cuts (Fig. 1). At times, these injuries may require medical examination because of the potential of subsequent infections, given kites' frequent foraging on rotting organic waste.



Fig. 1. A Black Kite takes off from its nest on a pylon to attack the photographer, who is standing on a balcony (Photo credit: F. Sergio).

4.2. Materials and Methods

Ethics statement

This research is part of a larger and long-term study on the demography of Black Kites in Delhi. We received the permits to conduct the fieldwork from the office of the Additional Principal Chief Conservator of Forests (APCCF), the Government of National Capital Territory of Delhi under the provisions of the Wildlife Protection Act, 1972 (permit number: CF/LC/105/07/HQ/10504-8). The Training, Research, and Academic Council (TRAC) of the Wildlife Institute of India, Dehradun (WII), gave bioethical approval for the research protocols. We performed all methods in accordance with the relevant guidelines and regulations laid out by TRAC WII with respect to study animal and human participants. We also sought informed consent from all the participants (or their legal guardians) for the semi-structured interviews (see below). We took all precautions to ensure researcher and animal safety, and maintained anonymity of the human respondents at all the stages of data recording during the field trials. All members of the field team were regularly administered with preventive vaccination, they wore thick hats/helmets and appropriate protective clothing so as to ensure safety.

Study Area

Delhi is a megacity of more than 16 million inhabitants, covering an area of 1500 km² and in constant expansion (Census of India, 2011). Three aspects of Delhi are important for kites. First, much of the city is characterized by poor solid waste management, which affords plenty of food to kites in the form of carrion or refuse. Second, many people engage in the centuries-old religious practice of feeding meat scraps to kites (hereafter termed 'ritualized-feeding'), typically offered by throwing meat into the air for the birds to catch. These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries (Pinault, 2008; Taneja, 2015). Whilst meat-offering is practiced by a number of communities, in Delhi it is especially prevalent amongst members of Islamic faith, whose numbers are concentrated in well-defined portions of the city (hereafter 'Muslim colonies') where large quantities of meat are tossed to kites at predictable hours each day, sometimes causing hundreds of kites to congregate. Third, Delhi retains reasonable green cover, thus providing abundant nesting habitat for kites (Paul & Nagendra, 2015)

Fieldwork procedures and statistical analysis

Data on attacks were collected during nest-checks in 2013-2016, conducted at 20 plots strategically scattered throughout the city in order to cover all its possible urban settings, from semi-natural to extremely built-up sites (see Kumar et al., 2014; Kumar et al., 2018) for details of plots and nest checks). On each occasion, nests were visited in a standardised manner: a team of three people approached the nest directly from a point approximately 50 m from the nest, chosen to be clearly visible to a kite perched in the nest area. One person (always the same one) then proceeded to climb the nest. A kite pair was classified as attacking when either of the two parents dive-bombed and made physical contact with any member of the team. To examine the characteristics that may affect the likelihood of aggression, we compared attacking and nonattacking pairs in the following manner. First, for each pair that attacked us, we chose a nonattacking pair that: (1) had eggs or chicks of similar age, (2) that was checked in the same year and on the same or preceding-following day, (3) that had received a similar number of previous visits by our team, and (4) that had a similar tree-arrangement configuration (nest in an isolated tree, line of trees, parkland or continuous woodland). This allowed us to investigate aggression while removing the potentially confounding effects of year, date, breeding stage, previous visit and local habitat-structure. Second, for all attacking and non-attacking pairs we collected a number of landscape and human variables (Supplementary Table S.1), based on our knowledge of kite ecology and of a previous study on habitat preferences by Delhi kites (Kumar et al., 2018). These variables estimated the structure and composition of the urban landscape around the nests, their local availability of organic garbage, their access to Muslim ritual-subsidies, the local density of humans around the nest and in the surrounding streets, and the close exposure to human presence through the presence-absence of an open balcony within 20 m of the nest (details in Supplementary Table S.1). Thus, they characterized each pair on the basis of its surrounding urban characteristics, food availability, and exposure to humans as well as their subsidies. Third, we used a logistic mixed model (Zuur et al., 2009), with pair-identity nested within plot-identity, to discriminate between attacking and non-attacking pairs on the basis of the landscape and human variables. To reduce collinearity and the number of variables presented to multivariate models, we employed the method of variable reduction proposed by Green (Green & Green, 1979). In this method, pairs of strongly intercorrelated variables (r >0.6) are considered as estimates of a single underlying factor. Only one of the two is retained for analysis, usually the one likely to be perceived as more important by the study organism. Of the remaining variables, only those for which significant univariate differences (P < 0.1) were detected between attacking and non-attacking pairs were included in the logistic model (Supplementary Table A.2). Univariate differences were carried out by means of t-tests and χ^2 tests. Model building was implemented through an information-theoretic approach, following recommendations by (Galipaud et al., 2014; Grueber et al., 2011; Richards et al., 2011). We used the "dredge" function of the MuMIn package to rank competing models on the basis of their weight and AICc (Grueber et al., 2011). Models within 3 AICc units of the top model were selected for model averaging, implemented through the MuMIn package. All the analyses were performed through Prog. R 3.4.3 (2013).

Finally, to gain an understanding of the extent and impact of attacks on local communities, we approached and interviewed all the people we encountered during our trials in the immediate proximity of the nests of attacking and non-attacking pairs (N = 278 interviews). This allowed us to test whether pairs that attacked us also had a higher probability of previously attacking local people, i.e. before and independently of our activities. Detailed analysis of the

interviews will be reported elsewhere, but in the Discussion, we delineate the main local opinions qualitatively, in order to place the conflict in the context of local attitudes. Throughout, all tests are two-tailed, statistical significance was set at ≤ 0.05 and means are given with 1 SE.

4.3. Results

To investigate the determinants of kites' attacks on humans, we recorded aggressive events during routine visits to kites breeding sites, in which nests were approached and examined by a team of three people in a standardized manner. Kites were classified as attacking when they dive-bombed and made physical contact with any member of the research team. In the four years of research, the percentage of attacking pairs averaged 25.5 % (range 18.0 - 37.7 %), and attacking individuals were present at 36 (i.e. 31.9 %) of 113 separate territories checked at least once for reproduction. Twenty-one of these 36 attacking pairs but none of the 36 non-attacking pairs had a history of past local attacks, as from interviews with local inhabitants ($\chi^2 = 15.09$, P < 0.0001), suggesting that pairs identified as aggressive by our trials were not responding to an unusual stimulus, but were already known to be problematic pairs well before our research activities. In all attacks during our trials, kites dive-bombed at high speed and tried to hit the target-person on the head, typically with the open hallux and closed phalanges, so as to either scratch or knock the target-person on the head. Due to escape movements, scratches were sometimes redirected on the forehead or on the neck or shoulders. All attacks were from behind and never when a person was staring at a kite dive-bombing towards the group.

To investigate the potential drivers of aggression, we built a logistic mixed model discriminating between attacking and non-attacking kites on the basis of a series of ecological, landscape and human socio-religious variables. In this model, the likelihood of attack increased with kite breeding success, with more human waste around the nest (higher hygiene score), with

higher access to Muslim subsidies, with higher human density in the streets and with the presence of a close-by balcony facing the nest (Table 1 and 2, Fig. 2). The interaction between balcony presence and access to Muslim subsidies was also important: kite aggression was more likely for pairs that had both a balcony close by and high access to Muslim subsidies (Fig. 3).



Fig. 2. The likelihood of attacking humans by a breeding Black kite pair increased with: its breeding success (panel a, left bars), with more human waste around its nest (higher hygiene score, panel a, central bars), with the presence of a balcony in close proximity of the pair's breeding site (panel a, right bars), with higher access to ritual subsidies from Muslim colonies (panel b), and with higher human density in the streets of the nest surroundings (panel c). Error bars represent 1 SE.



Fig. 3. Likelihood of aggressive attack on humans by nesting Black kites in relation to access to ritual-feeding sites (Muslim colonies) and the presence of a balcony within 20 m radius of the nest. Error bars represent 1 SE.

Table 1. Top ranking (i.e. with $\Delta AICc < 3$) generalised linear mixed models with binomial errors and a logit link function testing the effect of environmental, urban and human variables on likelihood of aggressive attack against humans (attacking vs control pair) by a nesting kite pair (N = 204 trials from 72 independent territories). Territory-identity nested within plot-identity was fitted as a random effect to all models. See Supplementary Table S.1 for the description of explanatory variables.

Explanatory variables in each model ^a	Degrees of	AICc	Delta	Model
	freedom		AICc	weight
Hygiene score + Breeding success	5	66.29	0.00	0.34
Balcony + Hygiene score + Breeding success +	8	67.77	1.48	0.16
Access to Muslim colonies + Balcony * Access to				
Muslim colonies				
Hygiene score + Breeding success + Access to	6	68.08	1.79	0.14
Muslim colonies				
Balcony + Hygiene score + Breeding success	6	68.18	1.89	0.13
Hygiene score + Urban cover + Breeding success	6	68.41	2.12	0.12
Human density + Hygiene score + Breeding success	6	68.48	2.19	0.11

^a Variables presented to the model: Number of people, Balcony, Urban cover, Green cover, Hygiene score, Human density, Access to Muslim colonies, Access to Muslim colonies * Hygiene score, Access to Muslim colonies * Urban cover, Access to Muslim colonies * Green cover, and Access to Muslim colonies * Balcony.

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Variable	$B \pm SE$	Z test	P value
Breeding Success	28.69 ± 7.33	3.91	< 0.0001
Hygiana scora	30.4 ± 7.0	3 86	0.0001
Trygiene score	50.4 ± 7.9	5.80	0.0001
Access to Muslim subsidies	1.31 ± 4.1	0.32	0.75
Balcony	8.57 ± 7.77	1.1	0.27
Balcony * Access to Muslim	17.19 ± 6.86	2.54	0.012
colonies			
Human density	1.14 ± 0.19	5.94	< 0.0001
Urban Cover	0.57 ± 7.46	0.08	0.94
Intercept	-76.2 ± 21.37	3.56	0.0003

Table 2. Model averaged coefficients for the explanatory variables that entered the top-ranking models of Table 1.

4.4. Discussion

Our results contribute to advance and integrate different fields of research such as ethnozoology, urban ecology and the resolution of human-wildlife conflicts. Below, we (1) explain the mechanisms that may generate the observed patterns and (2) discuss the importance of our findings for each of the above three disciplines.

Kite attacks on humans were not randomly distributed through the city and responded to a series of indicators of human activities, such as unhygienic management of waste disposal, Muslim ritual-feeding, and the intensity of human activity in the streets. This configuration of socio-religious features is preferred by the kites of Delhi because of its high food availability in the form of ritual subsidies and organic garbage (Kumar et al., 2018) and may have promoted aggression in three non-exclusive ways. First, kites feeding on ritual subsidies or organic waste (frequently accomplished side by side with indigent people digging for useful materials) are frequently in close proximity to people, which may have lowered their fear of humans. Second,

close proximity was frequently rewarded with food, which may have reinforced such loss of fear. Third, aggression varied with the interaction between access to Muslim ritual-subsidies and the presence of a balcony in the immediate proximity of the nest (Fig. 3). Thus, Muslim subsidies increased aggression-likelihood more markedly for pairs that nested in the immediate proximity of a balcony and, conversely, the presence of a balcony heightened aggression for pairs with ready access to Muslim subsidies. This suggests that peak aggression was promoted by the synergy of these two exposures to frequent and close encounters with humans.

In addition, human attacks were linked to successful reproduction. This could be promoted by two non-exclusive mechanisms: (1) parents could have a sense of the quality of their parental investment (e.g. based on their own or their offspring body condition) and defend more fiercely when success-prospects are high, as shown in other species (Montgomerie & Weatherhead, 1988; Redondo, 1989; Sergio & Bogliani, 2001) and (2) aggressive behaviour towards humans paralleled the capability to repel other more common nest predators, such as crows or monkeys (Kumar et al., 2014), leading to a lower probability of nest failure from predation. Independently of motivational or causational mechanisms, if human-attacking pairs are more productive, there is a possibility that such behaviour could become more frequent in the population in the future, particularly so if aggression propensity were genetically inherited or culturally transmitted (e.g. by young kites emulating their parents' defense tactics once adult).

Implications for urban ecology

Implications for urban ecology were clear and profound. First, kite aggression did not respond to landscape composition or other classical ecological variables, but rather to a series of socioreligious and cultural features. This represents a clear-cut example of the importance of integrating human cultural factors into research programs in urban ecology. While human presence and action is one of the most defining characteristics of urban ecosystems (Alberti, 2008), few studies on urban animals explicitly incorporate human culture and perceptions into their design (Grimm et al., 2000; Liu et al., 2007). When such aspects are tested, they are usually found to be key factors for urban ecology and conservation. For example, human socio-economic status has been shown to affect avian diversity, occurrence and distribution (Shaw et al., 2008; van Heezik & Hight, 2017; van Heezik et al., 2013), while human perceptions of affinity/aversion towards certain animals varied across an urban-rural gradient, with important repercussions for potential conservation action (de Oliveira et al., 2018).

Second, some studies have shown that bolder, more aggressive individuals are more likely to colonize urban environments (Carrete & Tella, 2011; Evans et al., 2010; Lowry et al., 2013; Møller, 2008). These links have usually been shown in comparisons of urban vs rural populations. If we consider the propensity to attack humans observed in this study as a measure of boldness, then our data extend this urban-rural comparison to individual variation within a city. Under this scenario, boldness in human tolerance may continue to be a key modulator of urban adaptation and exploitation even long after the initial colonization of the urban environment.

Third, the occurrence of the attacks in a highly-subsidized and thus high-density animal population coexisting with a dense human population generated a problem of unusual magnitude. First of all, only 25-30 % of kite pairs attacked humans, which compares with 19 and 73 % of Australian magpies Gymnorhina tibicen and Masked Lapwings Vanellus miles, two species also renowned for their attacks on humans in urban settings (Jones & Thomas, 1999; Lewis et al., 2015). However, even if only one in three or four pairs attacked humans, the local high density of kites over a very large area (average of 15 pairs/km²) (Kumar et al., 2014) implies that Delhi could easily hold over 5600 aggressive pairs. If we further consider that human density is high in Delhi and that attacking pairs were disproportionately concentrated in areas of higher human density, several thousand people could be potentially exposed to kites' attacks every year. For example, during our tests of approximately 20 min duration, there were on average 18 people in the immediate proximity of the nest of an attacking pair. If this figure is representative, then multiplying it by 5600 aggressive pairs would imply that more than 101,000 people could be passing/standing within attacking-radius of an aggressive kite pair basically in every given moment of the day. Furthermore, most of the pairs that attacked us had a clear history of past attacks on local inhabitants, implying that our type of deliberate nest intrusion did not somehow exaggerate the extreme attacks that we recorded. Attacking individuals were 'problematic' already well before our activities. Conflicts of this magnitude and concentration would be unlikely in any rural setting and underline how urban ecosystems may pose novel challenges and require new approaches to wildlife management and conservation (Ditchkoff et al., 2006).

Implications for research on human-wildlife conflict

This study confirmed and extended current knowledge on the drivers of human-attacks by vertebrate animals. First, habituation to human proximity and animal feeding have been frequently reported as drivers of aggression on humans by mammalian carnivores and primates (Bounds & Shaw, 1994; Fa, 1992; Hockings et al., 2010; McCullough,1982; Thompson et al., 2003). Our findings support these views, extend them to avian predators and thus suggest that they may represent generalized drivers of potential aggression across distantly related taxa. Second, human conflict with predators has often been associated with food scarcity driving low-quality, food-deprived individuals in close contact with humans (Graham et al., 2005; Lewis et al., 2015; Lindegren et al., 2018; Murray & St. Clair, 2017; Patterson et al., 2004; Torres et al., 2018).

In our case, attacks were concentrated in optimal, preferred habitat, and perpetrated by more productive, likely higher-quality individuals. Such dynamics may be more typical of synanthropic urban predators, whose high-quality individuals may be drawn to an abundant food supply but get habituated to humans in the process of accessing it. While food availability in both cases may mediate aggression, its enactment by individuals of different quality and breeding-potential may have strong repercussions for future trends in aggression rates, with obvious forecasting and management implications. This confirms the importance of resource-distribution in wildlife-human conflicts (Soulsbury & White, 2015; Blackwell et al., 2016) and further remarks how the management of synanthropic or urban wildlife may require specially-designed techniques (Ditchkoff et al., 2006).

Finally, social factors and cultural perceptions have been identified as important drivers of the intensity of human-wildlife conflict, but are seldom taken into consideration (Dickman, 2010; de Oliveira et al., 2018; Hazzah et al., 2009; Hockings et al., 2010; Kansky & Knight, 2014; Torres et al., 2018).Our results not only stressed the importance of socio-religious variables as key drivers of the conflict, but also show how they can enter the equally key humanpart of conflict resolution. In fact, despite the above-reported magnitude of the problem, interviews with 140 persons encountered under the nests of attacking pairs uncovered extremely positive attitudes of local inhabitants towards the birds, even by individuals who were previously injured (authors' unpubl. data). Overall, most people expressed fear for the attacks, as logically expected, but 100 % of the respondents justified and showed explicit sympathy for the kites. Sympathy was motivated in two ways: (1) kites were protecting their offspring (i.e. doing their duty of good parents), and (2) humans have destroyed and degraded natural habitats and wildlife has no option but to live with humans, implying the ultimate fault was of people rather than kites. In turn, local communities, all of them of either the Islamic or the Hindu faith, tied such empathy to religious views about kites and about wildlife in general. Muslims mainly revered kites as sort of sacred, given their role of "winged emissaries" that metaphorically take away towards the sky their sins, worries, or prayers, symbolized by the meat offered during ritual-feedings (Pinault, 2008; Taneja, 2015). Hindus believe that a soul undergoes body transformations, that all life forms are thus connected to one ultimate god form and thus they respected kites as part of their wider tolerance to all wildlife species as god's beings. Finally, positive attitudes were probably further promoted by the fact that (1) attacks only occurred during a minor, predictable part of the year (duration of about two months), (2) that most injuries were generally light due to local people learning to avoid certain sites, and (3) that people were

usually well aware of the useful ecosystem service provided to their neighbourhood by kites, which in Delhi remove more than 3900 tons of organic waste per year (authors' unpubl. data).

Whatever the underlying motivation, these positive attitudes clearly translated into actions. All people reported taking (non-harmful) action to avoid confrontations, which may further reinforce kite aggression through additional reward. This included avoiding the nest proximity, dissuading children from using the parks or certain sections of the park, or refraining from using the balcony until the nestlings fledged. Some schools and canteens have changed their rules to make children and customers eat their lunch inside the premises rather than outdoor close to an attacking pair. In one case, the husband of a woman who received a serious scratch on her face enclosed the balcony with a volleyball net in order to get protection while continuing to use the balcony. In all these cases, no attempts at retaliatory measures, such as nest removal or killing the birds, were ever noticed or reported. On few occasions, local inhabitants enquired the possibility that we could remove the nest, but strongly specifying that it would have to be done after the nestlings had fledged. They also asked information about whether there could be nonharmful ways to dissuade kites from nesting at specific locations and about how to behave so as to avoid being attacked. Note that such extreme tolerance, even after injury, would be extremely unlikely by denizens of the western world, where conflicts of similar kind often end up in court after retaliatory nest removals or illegal killings (Lees et al., 2013; Torres et al., 2018) and where urban people are often reported as disconnected from nature and profoundly puzzled by conflicts with wildlife, frequently seen as a nuisance to remove (Bjerke & Østdahl, 2004; Miller, 2005; Soulsbury & White, 2015; Sterba, 2012). Finally, to date, the few studies that have examined the role of human religion, ethnicity, or social factors in human-wildlife conflict have shown how they can shape human attitudes and perceptions and thus intervene on

the human side of the conflict (Dickman, 2010; de Oliveira et al., 2018; Hazzah et al., 2009; Hockings et al., 2010; Kansky & Knight, 2014; Torres et al., 2018) In our case, we show that they can also affect the animal side of the conflict-interaction by shaping animal aggression through reward and habituation, thus confirming and extending their importance.

Implications for ethnozoology and the importance of human cultural factors

Human socio-cultural factors permeated all results and allowed more realistic insights into the drivers of a human-wildlife conflict. In particular, kite attacks on humans responded to a geography of human religion, hygiene and poverty, and were concentrated within the productive sector of the kite population located at the high-end of the human-exploitation axis. Notably, kite behaviour was keenly adjusted to humans, tolerating them at close range when feeding but attacking them when provoked, while humans equally responded to kite behaviour, encouraging their ecosystem service function and avoiding them without retaliation when attacked. In this sense, kites and humans could be contextualized as participants in a "coupled-system" where each of the two actors co-shaped each other's socio-ecological space through repeated interactions, a phenomenon already suggested for other species (Clucas & Marzluff, 2011; Fuentes, 2012; Marzluff & Angell, 2005; Riley & Priston, 2010). Human culture was thus key to identifying drivers of attacks and problematic sectors of the city. It also intervened to alleviate the conflict, as current evidence suggested that, at present, the aesthetic, cultural, spiritual and ecosystem-service benefits offered by kites clearly outweighed the local, albeit diffuse discomfort provided by aggressive individuals. This highlights a growing appreciation of the value of intangible benefits provided by wildlife to humans (Cox & Gaston, 2016; Kansky & Knight, 2014; Keniger et al., 2013; Maller et al., 2006), but most of all, it shows how

ethnozoological approaches can improve ecological insight and bridge the gap between different disciplines such as behavioural ecology, wildlife management and urban ecology through direct incorporation of human socio-cultural aspects (Alves, 2012; Alves & Albuquerque, 2018). In fact, human-wildlife conflicts have been identified as prime examples of research and management activities where incorporation of socio-cultural tools is direly needed (Alberti, 2008; Alves & Albuquerque, 2018). In conclusion, given that many predatory vertebrates are likely to be attracted by subsidies from a growing human population worldwide (Newsome et al., 2015), conflicts promoted by close exposure to humans, as portrayed here, are likely to increase.
Acknowledgments

We thank Dr. R. Dor and two anonymous reviewers for constructive comments that greatly improved the manuscript, and Ujjwal Kumar and the Director, Dean and Research Coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Delhi Transport Corporation, Civic bodies of the Government of NCT of Delhi helped with legal permits, and the Director of the National Zoological Park of New Delhi gave access to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We thank Laxmi Narayan, Prince Kumar, Poonam and all the members of the "Black Kite Project Group" for help in the field, especially U. Gupta, H. Malhotra, A. Singh, P. Kumar, H. Singh, U. Nair and M. Singh. The project was funded by the Raptor Research and Conservation Foundation (Mumbai) and by the Govt. of India, Ministry of Environment, Forest and Climate Change. NK was funded by the Felix Scholarship Trust and Somerville College, Oxford University and FS by project CGL2015- 69445-P of the Spanish Ministry of Economy and Competitiveness with Feder Funds.

References

- Alberti, M. (2008). Advances in urban ecology: integrating humans and ecological processes in urban ecosystems (No. 574.5268 A4). New York: Springer.
- Alves, R. R. (2012). Relationships between fauna and people and the role of ethnozoology in animal conservation. *Ethnobiology and Conservation*, 1(2), 1-69.
- Alves, R. R. N., & Albuquerque, U. P. (2018). Introduction: Animals in Our Lives. In *Ethnozoology* (pp. 1-7).
- Bateman, P. W. & Fleming, P. A. (2012). Big city life: carnivores in urban environments. J. Zool. 287, 1-23
- Bhatia, S., Athreya, V., Grenyer, R., & Macdonald, D. W. (2013). Understanding the Role of Representations of Human–Leopard Conflict in Mumbai through Media- Content Analysis. *Conservation Biology*, 27(3), 588-594.
- Bird, D., Varland, D. & Negro, J. J. (1996). Raptors in human landscapes, Academic Press.
- Bjerke, T., & Østdahl, T. (2004). Animal-related attitudes and activities in an urban population. *Anthrozoös*, *17*(2), 109-129.
- Blackwell, B. F., DeVault, T. L., Fernández-Juricic, E., Gese, E. M., Gilbert-Norton, L., & Breck, S. W. (2016). No single solution: Application of behavioural principles in mitigating human–wildlife conflict. *Animal behaviour*, 120, 245-254.
- Bounds, D. L., & Shaw, W. W.(1994). Managing coyotes in U.S. national parks: human-coyote interactions. *Natural Areas Journal* 14, 280-284
- Carrete, M., & Tella, J. L. (2011). Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PloS one*, *6*(4), e18859.
- Census Organisation of India. (2011). Office of the Registrar General & Census Commissioner, India <u>http://censusindia.gov.in/2011census</u>
- Clucas, B., & Marzluff, J. M. (2011). Coupled relationships between humans and other organisms in urban areas. Urban ecology: patterns, processes, and applications, 135-147.

- Conover, M. R. (1997). Wildlife management by metropolitan residents in the United States: practices. *perceptions, costs. and values. Wildlife Society Bulletin, 25*, 306-311.
- Conover, M. R. (2001). Resolving human-wildlife conflicts: the science of wildlife damage management. CRC press.
- Cox, D. T., & Gaston, K. J. (2016). Urban bird feeding: connecting people with nature. *PloS* one, 11(7), e0158717.
- Cypher, B. L., Phillips, S. E., & Kelly, P. A. (2013). Quantity and distribution of suitable habitat for endangered San Joaquin kit foxes: conservation implications. *Canid Biology and Conservation*, *16*, 25-31.
- de Oliveira, J. V., de Faria Lopes, S., Barboza, R. R. D., & da Nóbrega Alves, R. R. (2018). To preserve, or not to preserve, that is the question: urban and rural student attitudes towards wild vertebrates. *Environment, Development and Sustainability*, 1-19.
- Dickman, A. J., Hazzah, L., Carbone, C., & Durant, S. M. (2014). Carnivores, culture and 'contagious conflict': Multiple factors influence perceived problems with carnivores in Tanzania's Ruaha landscape. *Biological Conservation*, *178*, 19-27.
- Dickman, A. J. (2010). Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Animal conservation*, *13*(5), 458-466.
- Ditchkoff, S. S., Saalfeld, S. T., & Gibson, C. J. (2006). Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban ecosystems*, 9(1), 5-12.
- Elliot, E. E., Vallance, S., & Molles, L. E. (2016). Coexisting with coyotes (Canis latrans) in an urban environment. *Urban ecosystems*, *19*(3), 1335-1350.
- Evans, J., Boudreau, K., & Hyman, J. (2010). Behavioural syndromes in urban and rural populations of song sparrows. *Ethology*, *116*(7), 588-595.
- Fa, J. E. (1992). Visitor- directed aggression among the Gibraltar macaques. *Zoo Biology*, *11*(1), 43-52.
- Fascione, N., Delach, A., & Smith, M. E. (2004). Introduction: People and Predator: from conflict to coexistence. *People and Predators: From Conflict to Coexistence*.

- Ferguson-Lees, J., & Christie, D. A. (2001). Monk vulture: Aegypius monachus. *Raptors of the World*, 437-438.
- Francis, R. A., & Chadwick, M. A. (2012). What makes a species synurbic?. *Applied Geography*, 32(2), 514-521.
- Fuentes, A. (2012). Ethnoprimatology and the anthropology of the human-primate interface. *Annual Review of Anthropology*, *41*, 101-117.
- Galbreath, D. M., Ichinose, T., Furutani, T., Yan, W., & Higuchi, H. (2014). Urbanization and its implications for avian aggression: a case study of urban black kites (Milvus migrans) along Sagami Bay in Japan. *Landscape ecology*, *29*(1), 169-178.
- Galipaud, M., Gillingham, M. A., David, M., & Dechaume- Moncharmont, F. X. (2014). Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. *Methods in Ecology and Evolution*, 5(10), 983-991.
- Gaston, K. J., Davies, Z. G., & Edmondson, J. L. (2010). Urban environments and ecosystem functions. *Urban ecology*, 35-52.
- Gehrt, S. D., Riley, S. P., & Cypher, B. L. (Eds.). (2010). Urban carnivores: ecology, conflict, and conservation. JHU Press.
- Graham, K., Beckerman, A. P., & Thirgood, S. (2005). Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation*, *122*(2), 159-171.
- Green, R. H., & Green, R. M. (1979). Sampling design and statistical methods for environmental biologists. John Wiley & Sons.
- Grimm, N. B., Grove, J. G., Pickett, S. T., & Redman, C. L. (2000). Integrated approaches to long-term studies of urban ecological systems: Urban ecological systems present multiple challenges to ecologists—Pervasive human impact and extreme heterogeneity of cities, and the need to integrate social and ecological approaches, concepts, and theory. *AIBS Bulletin*, 50(7), 571-584.
- Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *Journal of evolutionary biology*, 24(4), 699-711.

- Hadidian, J. (2015). Wildlife in US cities: managing unwanted animals. *Animals*, 5(4), 1092-1113.
- Hazzah, L., Mulder, M. B., & Frank, L. (2009). Lions and warriors: social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. *Biological Conservation*, 142(11), 2428-2437.
- Hazzah, L., Bath, A., Dolrenry, S., Dickman, A., & Frank, L. (2017). From attitudes to actions: predictors of lion killing by Maasai warriors. *PloS one*, *12*(1), e0170796.
- Hockings, K. J., Yamakoshi, G., Kabasawa, A., & Matsuzawa, T. (2010). Attacks on local persons by chimpanzees in Bossou, Republic of Guinea: long- term perspectives. *American Journal of Primatology*, 72(10), 887-896.
- Hosey, G., & Melfi, V. (2014). Human-animal interactions, relationships and bonds: a review and analysis of the literature. *International Journal of Comparative Psychology*, 27(1).
- Jones, D. N., & Thomas, L. K. (1999). Attacks on humans by Australian magpies: management of an extreme suburban human-wildlife conflict. *Wildlife Society Bulletin (1973-2006)*, 27(2), 473-478.
- Kansky, R., & Knight, A. T. (2014). Key factors driving attitudes towards large mammals in conflict with humans. *Biological Conservation*, *179*, 93-105.
- Kellert, S. R. (1980). American-Attitudes Toward and Knowledge of Animals an Update. International Journal for the Study of Animal Problems, 1(2), 87–119. 24. Timm, R. M., Baker, R. O., Bennett, J. R., & Coolahan, C. C. (2004). Coyote attacks: an increasing suburban problem.
- Keniger, L. E., Gaston, K. J., Irvine, K. N., & Fuller, R. A. (2013). What are the benefits of interacting with nature?. *International journal of environmental research and public health*, 10(3), 913-935.
- Kofron, C. P. (1999). Attacks to humans and domestic animals by the southern cassowary (Casuarius casuarius johnsonii) in Queensland, Australia. *Journal of Zoology*, 249(4), 375-381.
- Kumar, N., Mohan, D., Jhala, Y. V., Qureshi, Q., & Sergio, F. (2014). Density, laying date, breeding success and diet of Black Kites Milvus migrans govinda in the city of Delhi (India). *Bird study*, 61(1), 1-8.

- Kumar, N., Gupta, U., Jhala, Y. V., Qureshi, Q., Gosler, A. G., & Sergio, F. (2018). Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools. *Urban Ecosystems*, 21(2), 339-349.
- Kushnir, H., Leitner, H., Ikanda, D., & Packer, C. (2010). Human and ecological risk factors for unprovoked lion attacks on humans in southeastern Tanzania. *Human Dimensions of Wildlife*, 15(5), 315-331.
- Kushnir, H., Weisberg, S., Olson, E., Juntunen, T., Ikanda, D., & Packer, C. (2014). Using landscape characteristics to predict risk of lion attacks on humans in south- eastern Tanzania. *African journal of ecology*, 52(4), 524-532.
- Lees, D., Sherman, C. D., Maguire, G. S., Dann, P., Cardilini, A., & Weston, M. A. (2013). Swooping in the suburbs; parental defence of an abundant aggressive urban bird against humans. *Animals*, 3(3), 754-766.
- Lewis, D. L., Baruch-Mordo, S., Wilson, K. R., Breck, S. W., Mao, J. S., & Broderick, J. (2015). Foraging ecology of black bears in urban environments: guidance for human- bear conflict mitigation. *Ecosphere*, 6(8), 1-18.
- Lindegren, L., Hernandez, J., Bombrun, A., Klioner, S., Bastian, U., Ramos-Lerate, M., ... & Lammers, U. (2018). Gaia Data Release 2: The astrometric solution. *arXiv preprint arXiv:1804.09366*.
- Liu, J., Dietz, T., Carpenter, S. R., Alberti, M., Folke, C., Moran, E., ... & Ostrom, E. (2007). Complexity of coupled human and natural systems. *science*, *317*(5844), 1513-1516.
- Lowry, H., Lill, A., & Wong, B. B. (2013). Behavioural responses of wildlife to urban environments. *Biological reviews*, 88(3), 537-549.
- Maller, C., Townsend, M., Pryor, A., Brown, P., & St Leger, L. (2006). Healthy nature healthy people: 'contact with nature' as an upstream health promotion intervention for populations. *Health promotion international*, *21*(1), 45-54.
- Marzluff, J. M., & Angell, T. (2005). Cultural coevolution: how the human bond with crows and ravens extends theory and raises new questions. *Journal of Ecological Anthropology*, 9(1), 69-75.

- Marzluff, J. M., Shulenberger, E., Endlicher, W., Alberti, M., Bradley, G., Ryan, C., ... & ZumBrunnen, C. (2008). An International Perspective on the Interaction Between Humans and Nature. Springer Science and Business Media, New York.
- McCullough, D. R. 1982. Behavior, bears, and humans. Wildl Soc Bull 10:27-33
- Messmer, T. A. (2000). The emergence of human-wildlife conflict management: turning challenges into opportunities. *International Biodeterioration & Biodegradation*, 45(3-4), 97-102.
- Miller, J. R. (2005). Biodiversity conservation and the extinction of experience. *Trends in ecology & evolution*, 20(8), 430-434.
- Montgomerie, R. D., & Weatherhead, P. J. (1988). Risks and rewards of nest defence by parent birds. *The Quarterly Review of Biology*, *63*(2), 167-187.
- Møller, A. P. (2008). Flight distance of urban birds, predation, and selection for urban life. *Behavioral Ecology and Sociobiology*, 63(1), 63.
- Murray, M. H., & St. Clair, C. C. (2017). Predictable features attract urban coyotes to residential yards. *The Journal of Wildlife Management*, 81(4), 593-600.
- Naoroji, R. (2006). Birds of prey of the Indian subcontinent. Christopher Helm.
- Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J., & Dickman, C. R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, 24(1), 1-11.
- Nyhus, P. J., & Tilson, R. (2004). Characterizing human-tiger conflict in Sumatra, Indonesia: implications for conservation. *Oryx*, *38*(1), 68-74.
- Parker, J. W. (1999). Raptor attacks on people. Journal of Raptor Research, 33, 63-66.
- Patterson, B. D., Kasiki, S. M., Selempo, E., & Kays, R. W. (2004). Livestock predation by lions (Panthera leo) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological conservation*, 119(4), 507-516.
- Paul, S., & Nagendra, H. (2015). Vegetation change and fragmentation in the mega city of Delhi: Mapping 25 years of change. *Applied Geography*, 58, 153-166.

- Pinault, D. (2008). Raw meat skyward: pariah-kite rituals in Lahore. *Equinox Publishing*, 108-121.
- Redondo, T. (1989). Avian nest defence: theoretical models and evidence. *Behaviour*, 111(1), 161-195.
- Redpath, S. M., Young, J., Evely, A., Adams, W. M., Sutherland, W. J., Whitehouse, A., ... & Gutierrez, R. J. (2013). Understanding and managing conservation conflicts. *Trends in ecology & evolution*, 28(2), 100-109.
- Richards, S. A., Whittingham, M. J., & Stephens, P. A. (2011). Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology*, 65(1), 77-89.
- Riley, E. P., & Priston, N. E. (2010). Macaques in farms and folklore: exploring the humannonhuman primate interface in Sulawesi, Indonesia. *American Journal of Primatology*, 72(10), 848-854.
- Rutz, C. (2008). The establishment of an urban bird population. J. Anim. Ecol. 77: 1008-1019
- Sergio, F., & Bogliani, G. (2001). Nest defense as parental care in the northern hobby (*Falco subbuteo*). *The Auk*, *118*(4), 1047-1052.
- Shaw, L. M., Chamberlain, D., & Evans, M. (2008). The House Sparrow Passer domesticus in urban areas: reviewing a possible link between post-decline distribution and human socioeconomic status. *Journal of Ornithology*, 149(3), 293-299.
- Siemer, W. F., Hart, P. S., Decker, D. J., & Shanahan, J. E. (2009). Factors that influence concern about human-black bear interactions in residential settings. *Human Dimensions* of Wildlife, 14(3), 185-197.
- Soulsbury, C. D., & White, P. C. (2015). Human–wildlife interactions in urban areas: a review of conflicts, benefits and opportunities. *Wildlife Research*, 42(7), 541-553.
- Sterba, J. (2012). *Nature wars: the incredible story of how wildlife comebacks turned backyards into battlegrounds*. Crown Pub.
- St John, F. A., Keane, A. M., Edwards-Jones, G., Jones, L., Yarnell, R. W., & Jones, J. P. (2011). Identifying indicators of illegal behaviour: carnivore killing in human-managed

landscapes. *Proceedings of the Royal Society B: Biological Sciences*, 279(1729), 804-812.

- Sudarshan, M. K., Madhusudana, S. N., Mahendra, B. J., Rao, N. S. N., Narayana, D. A., Rahman, S. A., ... & Ravikumar, K. (2007). Assessing the burden of human rabies in India: results of a national multi-center epidemiological survey. *International Journal* of Infectious Diseases, 11(1), 29-35.
- Taneja, A. V. (2015). Saintly animals: the shifting moral and ecological landscapes of North India. *Comparative Studies of South Asia, Africa and the Middle East*, *35*(2), 204-221.
- Team, R. R. (2013). Development Core Team. R: A Language and Environment for Statistical Computing. R foundation for statistical computing.
- Thompson, J., Shirreffs, L., & McPhail, I. (2003). Dingoes on Fraser Island—tourism dream or management nightmare. *Human Dimensions of Wildlife*, 8(1), 37-47.
- Thornton, C., & Quinn, M. S. (2009). Coexisting with cougars: public perceptions, attitudes, and awareness of cougars on the urban-rural fringe of Calgary, Alberta, Canada. *Human-Wildlife Conflicts*, *3*(2), 282-295.
- Tidemann, S., & Gosler, A. (2012). *Ethno-Ornithology: birds, indigenous peoples, culture and society*. Earthscan.
- Timm, R. M., Baker, R. O., Bennett, J. R., & Coolahan, C. C. (2004). Coyote attacks: an increasing suburban problem.
- Torres, D. F., Oliveira, E. S., & Alves, R. R. (2018). Conflicts Between Humans and Terrestrial Vertebrates: A Global Review. *Tropical Conservation Science*, *11*, 1940082918794084.
- van Heezik, Y., Freeman, C., Porter, S., & Dickinson, K. J. (2013). Garden size, householder knowledge, and socio-economic status influence plant and bird diversity at the scale of individual gardens. *Ecosystems*, 16(8), 1442-1454.
- van Heezik, Y., & Hight, S. R. (2017). Socio-economic-driven differences in bird-feeding practices exacerbate existing inequities in opportunities to see native birds in cities. *Journal of Urban Ecology*, 3(1), jux011.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models and extensions in ecology with R. New York: Springer. *574 p*.

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Supplementary Tables

Supplementary Table S.1. Ecological, landscape and human variables used to characterize Black kite attacking and non-attacking pairs within the city of Delhi (India).

Variable	Description
Number of people	Number of people (not belonging to the field-team) within 50 m of the nest at the beginning of the attack
	trial (e.g. sitting in a park, playing, walking in the street, etc.)
Number of offspring	Number of eggs or chicks in the nest at the time of the kite attack trial
Breeding Success	Categorical variable: 0 = failed breeding attempt, 1 = successful breeding attempt. An attempt was
	classed as successful if the pair managed to raise at least one nestling to fledging age (40-48 days old).
NND5 (m)	Mean of the distance to the five closest kite neighbours
Territories within 200 m	Number of territories occupied within 200 m of the target nest
Colony size	Number of nests within the kite colony
Balcony	Categorical variable: 0 = absence, 1 = presence of a balcony within 20 m of the sampled nest
Index of road density	Number of asphalted roads crossed by a 500 m north-south and a 500 m east-west transect crossing each
	other on the nest
Urban cover	Percentage area covered by built-up structures (buildings, roads, parking lots, or any other impervious
	surface) within 500 m of the nest
Green cover	Percentage area covered by shrub/tree vegetation within 500 m of the nest
Hygiene score	Level of sanitation: 1 = clean areas; 2 = areas under poor waste management regime ^a
Human density	Average number of people walking within 2m of a stationary observer during 5 min at 10 locations
	randomly plotted within 200 m of the nest ^b
Access to Muslim subsidies	First component (PC1) of a principal component analysis on Muslim density and on the proximity to the
	three closest Muslim colonies (following Kumar et al. ³⁹).

^a Categorical variable with two levels: 1 = efficient waste disposal with very scarce or no organic refuse in the streets; 2 = abundant and widespread refuse in the streets throughout the area, either in small frequent piles, in illegal ephemeral dumps, or as individual items scattered a bit of everywhere through all streets (following Kumar et al.⁵⁰).

^b Counts were only operated between 10:00-17:00 hrs and avoided during atypical, momentary peak periods of human traffic, such as exits from work or schools, in order to maintain consistency across sites (following Kumar et al.⁵⁰).

Supplementary Table S.2. Mean (± 1 SE) estimates of variables measured at 36 Black Kite pairs that attacked humans for nest defense and at 36 control pairs for which no attacks were observed. Differences between the two samples were tested by means of t-tests, or χ^2 tests for categorical variables. Symbols: * P < 0.05; ** P < 0.01; *** P < 0.001.

Variable	Attacking pairs	Non-attacking pairs
Offspring number ***	1.89 ± 0.10	1.32 ± 0.10
Breeding Success ^{a, b} ***	85.29 %	42.15 %
Index of road density ^b	7.52 ± 0.24	7.40 ± 0.34
Urban cover ^b ***	0.46 ± 0.02	0.35 ± 0.02
Green cover ^b **	0.23 ± 0.01	0.31 ± 0.02
Balcony ^{b, c} ***	61.76 %	24.51 %
NND5 (m) *	156.31 ± 10.75	197.58 ± 16.66
Territories within 200 m	9.89 ± 0.61	8.85 ± 0.58
Colony size	5.67 ± 0.34	4.92 ± 0.31
Number of people ^b ***	18.05 ± 1.47	8.96 ± 0.83
Hygiene score ^{b, d} ***	87.25 %	54.90 %
Human density ^b ***	17.38 ± 1.19	11.49 ± 0.72
Access to Muslim subsidies ^b **	0.39 ± 0.11	-0.19 ± 0.07

^a Percentage of nests which raised at least one nestling to fledging age (40-48 days old).

^b Variable fitted to the multivariate models of Table 1.
^c Percentage of nests which had a balcony within a 20 m radius.
^d Percentage of locations with poor sanitation.

The population density of an urban predator is inextricably tied to human cultural practices

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This chapter is currently submitted to a high-ranking journal with a broad ecological audience.

• Submitted typesetting included in the Appendix

Human socio-cultural factors are recognized as fundamental drivers of urban ecological processes, but their effect on wildlife is still poorly known. In particular, human cultural aspects may differ substantially between the extensively studied urban settings of temperate regions and the poorly-studied cities of the tropics, which may thus offer profoundly different niches for urban wildlife. Here, we report how the population-levels of a scavenging raptor which breeds in the megacity of Delhi, the Black kite *Milvus migrans*, depend on spatial variation in human subsidies, mainly in the form of philanthropic offerings of meat given for religious purposes. This tight connection with human culture, which generated the largest raptor concentration in the world, was modulated further by breeding-site availability. The latter constrained the level of resource-tracking by the kites and their potential ecosystem service, and could be used as a density-management tool. Similarities between animal population-densities, key anthropogenic resources and human beliefs may occur in thousands of cities all over the globe and may fit poorly with our current understanding of urban ecosystem functioning. For many urban animals, key resources are inextricably linked with human culture, an aspect that has been largely overlooked.

Keywords: human culture; human subsidies; nest availability; population limitation; tree management; urban raptor

5.1. Introduction

Urbanization is one of the most rapidly expanding land uses worldwide (Malakoff et al., 2016; United Nations, 2014), with profound consequences for animal individuals, populations and communities (Gaston, 2010; Marzluff et al., 2008; Niemelä et al., 2011). As a result, research in urban ecology is in rapid expansion (e.g. Niemelä et al., 2011), but three aspects have received very limited attention. First, current knowledge is heavily biased towards urban systems of Europe and North America, despite the fact that a major share of urban sprawl is taking place in tropical countries (Grimm et al., 2008; Malakoff et al., 2016) and that these may present profoundly different human and ecological settings from their temperate counterparts. Thus, there have been many calls highlighting the urgent need for more studies from tropical cities, but with limited progress (e.g. Magle et al., 2012; Marzluff, 2016). Secondly, despite the fact that humans are, for obvious reasons, the dominant species in the urban ecosystem, few studies have incorporated explicit human socio-cultural aspects in their research. Such factors are increasingly recognized as essential components of the urban ecosystem, leading to an urgent need for more insight into their ecological consequences (Alberti et al., 2003; Alberti, 2008; Shochat et al., 2006). In particular, while some studies have reported biodiversity, or individuallevel behavioral responses by urban animals to human socio-cultural factors (e.g. Kinzig et al., 2005; Kumar et al., 2018b), it is virtually unknown whether these translate into population-level consequences. Thirdly, while much research has focused on the relationship between animal abundance and urbanization, this has been framed mainly as: (1) comparisons of population density between urban and rural sites; or (2) evaluations of the landscape predictors of density measured within small vegetation patches (e.g. parks) embedded within the urban matrix of impervious surfaces (reviews in Gaston, 2010; Marzluff et al., 2008; Niemelä et al., 2011). In

the latter case, the small size of these fragments enforced that density could only be studied for small-bodied species, such as many songbirds. Both these approaches are obviously valuable to tackle the factors that allow certain species to colonize or persist in urban environments, but miss important information on: (1) density variations within the urban matrix and within the fully urban core of a city landscape, which is still typically heterogeneous (Forman, 2014) and could impose further internal variations in density; and (2) density variations of wide-ranging species, such as raptors, whose populations may respond to integrated components of the landscape that include both the urban matrix and its embedded patches of "natural" habitats, but may not fit well a simplistic classification such as urban vs rural.

Thus, there is a need for studies from tropical areas that investigate whether the density of wide-ranging species capable of urban colonization responds to variation in urban configuration and human socio-cultural factors. To fill this gap of knowledge, here we examine how the population abundance of a raptor, the Black kite *Milvus migrans*, breeding in a tropical megacity responds to variation in landscape features and human cultural factors that mediate food and nest-site availability.

Raptors are upper-trophic-level, wide-ranging predators. Many species of this avian group have recently been shown to be able to colonize and even thrive in urban areas, by attraction to abundant prey supplies usually directly or indirectly promoted by human subsidies (Boal & Dykstra, 2018). Raptor populations are typically limited by food and nest sites (Newton, 1979), both of which are likely to depend in urban areas on structural landscape features and human socio-economic processes. However, it is virtually unknown whether the population levels of these species vary among different types of urban configuration, or in response to human cultural factors. Such a lack of knowledge is likely caused by the low density of these species

and the consequent challenges to survey enough study areas of sufficient size to investigate variations in density and link them to urban features.

5.2. Materials and Methods

Model species

The Black kite (hereafter "kite") is a medium-sized, opportunistic predator and facultative scavenger. In India, the resident subspecies *M. m. govinda* is synurbic (Francis & Chadwick, 2012), i.e. it occurs almost exclusively in close association with humans in towns and cities (Naoroji, 2006). In Delhi, where this study was conducted, kites breed throughout the city, often a few meters from human habitation, thanks to the exploitation of human food subsidies facilitated by inefficient refuse disposal and by religious kite-feeding practices (Fig. 1, Kumar et al., 2014; 2018a; see details below). While kites over-select breeding-sites with ready access to such subsidies (Kumar et al. 2018a), it is currently unknown whether this generates heterogeneity in breeding distribution at the population level, especially once controlling for nest-site availability. Overall, the large area of this megacity and the magnitude of its food subsidies for kites generate one of the largest raptor concentrations of the world (Kumar et al., 2014). In turn, this offers a unique opportunity to examine how a predator population density varies among city-sectors which differ in access to religious subsidies, landscape configuration and availability of nesting structures.

Study Area

Delhi is a megacity of more than 16 million inhabitants, covering an area of 1500 km² and in constant expansion (http://censusindia.gov.in/2011census). Three aspects of Delhi are important for kites. First, much of the city is characterized by poor solid waste management, which affords plenty of food to kites in the form of carrion or refuse. Secondly, many people engage in the centuries-old religious practice of feeding meat scraps to kites (hereafter termed 'ritualized-feeding'), typically offered by throwing meat into the air for the birds to catch (Fig. 1). These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries (Pineault, 2008; Taneja, 2015). Whilst meat-offering is practiced by a number of communities, in Delhi it is especially prevalent amongst members of the Islamic faith, whose numbers are concentrated in well-defined portions of the city (hereafter 'Muslim colonies') where large quantities of meat are tossed to kites at predictable hours each day, sometimes causing hundreds of kites to congregate. Third, Delhi still retains reasonable green cover, thus providing abundant nesting habitat for kites (Paul & Nagendra, 2015). However, tree cover is also being rapidly lost (Paul & Nagendra, 2015), which calls for the need to forecast the potential ecological consequences of such changes.

Field procedures

We surveyed kite nests systematically in 2013-2018 at 28 plots of approximately 1 km². These were plotted strategically (randomly stratified) within Delhi (1500 km²) so as to cover all its possible urban settings, from semi-natural to extremely built-up sites (details in Kumar et al., 2014). We surveyed each plot by walking slowly and carefully inspecting all potential nest structures (trees, poles, towers etc.). Structures were classified as active nest-sites when a kite

individual or pair was observed to perch on a nest or its immediate surroundings, or to add material to a nest. Each plot was surveyed \geq three successive times each year during the breeding season, separated by \geq 20 days until we were reasonably confident to have detected all territorial pairs. This generated an overall sample of 79 plot-years available for analysis. To measure nestsite availability for each plot, we: (1) digitized all large-enough trees clearly visible in Google Earth imagery; (2) visited each plot and mapped any additional trees that were not visible in Google Earth (e.g. because of low quality, blurred imagery for some sectors of Delhi) and all potential anthropogenic nest-structures (e.g. poles, towers) that were typically too difficult to detect in Google Earth. Because more than 90 % of the available nest-structures were trees, we summed trees and artificial structures into a single cumulative estimate of breeding-site availability.

Statistical analyses

To investigate the predictors of kite population-density, for each plot we collected a number of landscape and human variables (Table S1) chosen on the basis of our knowledge of kite ecology and of previous analyses of the factors that affect habitat preferences, breeding success and behavioural performance by Delhi kites (Kumar et al. 2018a,b, 2019). These variables characterized each plot in terms of its landscape structure, food availability (e.g. local availability of organic garbage, access to Muslim ritual-subsidies), and nest-site availability (details in Table S1). We further hypothesized that the effect of food availability could interact with nest availability in shaping density (e.g. Newton, 2013) and thus also modelled the interaction of nest availability with Muslim subsidies or with refuse availability. We then tested the effect of the above variables on kite density as follows. Because density could be spatially

autocorrelated, we initially modelled it through a spatial linear mixed model by means of a Bayesian approach, as outlined in Zuur et al. (2017). However, such a model gave poor support to the presence of spatial autocorrelation and gave the same conceptual results (Appendix S1). Thus, we repeated the analysis by means of a linear mixed model (LMM) with normal errors and an identity link (Zuur et al., 2009), where plot-identity was fitted as a random factor. The LMM was built through a backward stepwise procedure following Zuur et al. (2009): all explanatory variables were fitted to a maximal model, extracted one at a time, and the associated change in model deviance was assessed by the significance of a likelihood-ratio test; the procedure was repeated until we obtained a final model which only included significant variables (Zuur et al., 2009). The R^2 of the LMM was calculated following Nakagawa and Schielzeth (2013). Variables were standardized before fitting them to the models and all analyses were performed through R 3.4.3 (R Development Core team, 2017).

5.3. Results

The average density in Delhi was 19.02 breeding pairs/km² (SE = 7.43, n = 28 independent plots). Kite density increased with deteriorating sanitation levels (i.e. more human refuse in the streets) and depended on the interaction between access to Muslim subsidies and nest-site availability (Table 1): density increased more steeply with Muslim subsidies when breeding sites were abundant than when they were in poor supply (Fig. 1). These explanatory variables explained 89.9 % of the variation in density (Fig. 2).

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Table 1. Linear mixed model with normal errors and an identity link function testing the effect of landscape and human variables on the population density of Black kites in the megacity of Delhi (India).

Variable	$B \pm SE$	t	Р
Access to Muslim subsidies	6.07 ± 4.25	1.43	0.166
Refuse availability score	16.18 ± 6.80	2.38	0.025
Nest-site availability	29.87 ± 5.57	5.36	< 0.001
Access to Muslim subsidies * Nest-site availability	13.10 ± 4.90	2.67	0.010
Intercept	13.19 ± 3.53	3.74	0.010



Fig. 1. The Black kites of Delhi depend heavily on human subsidies offered for religious reasons: (a) a man with his two sons ritually feeds kites with the typical, compact chunks of red meat (red circle); (b) large numbers of kites, sometimes into the hundreds, may congregate at such feeding events; (c) the ritual offerings are taken to the nests; (d) a parent kite is about to feed its fledgling with a ritual meat chunk. More than 90 % of the diet in this population is composed of ritual offerings, which explains the tight link between breeding density and ready access to human cultural subsidies (Photo credit for all images: F. Sergio).

Fig. 2. The population density of Black kites in the megacity of Delhi (India) increases with food availability (access to Muslim subsidies), but such relationship is modulated by the availability of breeding-sites. For clarity of visualization, nest availability is here depicted as high (above the median value of nest availability: black dots, continuous line) or low (below the median value: white dots, hatched line).



Access to Muslim subsidies

5.4. Discussion

Kite density was tied to spatial variation in human subsidies, in the form of human refuse, ritual offerings and their ready accessibility. Because kite breeding pairs were previously shown to select sites with these same characteristics (Kumar et al., 2018a), individual-level habitat selection scaled up to population-level consequences. However, the subsidy-effect on density was more complex, because it was also modulated by breeding-site availability. Higher nest-site availability allowed the population to increase more steeply and reach higher densities in response to religious subsidies (Fig. 1). Conversely, lower nest availability constrained the breeding population to a weaker response to religious subsidies (Fig. 1). Thus, the availability of nesting structures modulated the capability of the population to track its food resources. As a consequence, only the combination of high availability of both human subsidies and urban nesting structures (trees, artificial poles and towers) allowed the population to reach the extremely high densities that generate what is probably the largest raptor concentration in the world.

The above results are important for two reasons. First, most of the support for the limitation of animal populations by breeding site availability is given by experimental studies based on nest-box addition-removals (reviews in Newton 1998, 2013). For species that build their own nests, demonstrations of the importance of nest availability are scarcer, probably because measuring the availability of nesting structures is often difficult or very time consuming. In urban settings in particular, we are not aware of previous studies showing links between population density and breeding-site availability, despite their obvious importance for management in the highly "engineered" landscape of urban ecosystems. Secondly, while the importance of human subsidies for predator populations is well established (e.g. Newsome et

al., 2014; Oro et al., 2013), the fact that breeding-site availability can mediate their populationeffect is, to our knowledge, reported here for the first time, and could be exploited for management purposes (see below).

Overall, our results showed how the density of an urban raptor was limited by food and nestsites, whichever was in shorter supply. This suggested the action of processes of population functioning in urban settings broadly similar to those observed in more natural habitats (e.g. Newton 1979, 1998, 2013), but their modality and underlying mechanism stood out strikingly in that food was dictated by the spatial zoning of human socio-religious and cultural practices. This stresses the importance of human behaviours and culture as an interactive component of the urban ecosystem (Alberti 2008). In fact, for synanthropic species that have closely coexisted with man in cities for centuries and are thus in the mature stages of urban colonization, humans can become a targeted resource and the leading component of their ecological niche, rather than a constraint to avoid or withstand. For example, in our population more than 90 % of the diet was dominated by ritual subsidies (unpubl. data from > 1000 prey items from camera-trapping at 40 nests).

To date, other studies have reported the effect of human socio-economic factors on the behaviour of the individuals of certain species (e.g. van Heezig & Hight, 2017; Kumar et al., 2018b) or on the biodiversity of gardens and parks embedded in the urban matrix (e.g. Kinzig et al., 2005; van Heezig et al., 2013). Here, we show that these individual and local effects can scale-up to population-level responses. This highlights how human practices and culture, which are often spatially clustered in cities for socio-economic and historical reasons (Kinzig et al., 2005), can structure the urban landscape, ultimately creating ecologically-relevant social gradients which are independent and overlaid over more classical gradients based on urban

physical structures (e.g. housing density) or position along an urban-rural transition. Such sociocultural gradients are often challenging to detect and to measure, because they may not be reflected by any strikingly visible or physical feature (Faeth et al., 2005). However, the fact that their modelling explained nearly 90 % of the variation in kite density and that diet was so dominated by religious offerings provides compelling support for the often stressed need to incorporate a sociological perspective into studies in urban ecology (Alberti et al., 2003, 2008; Grimm et al., 2008; Marzluff et al., 2008). In particular, we emphasize that socio-economic and cultural gradient is likely to be present in most cities of the world. In the much studied cities of Europe and North America, such gradients often reflect differences in income and social status (e.g. Kinzig et al. 2005), while our study completes this picture by showing gradients based on religious factors, sanitary conditions and refuse management. These latter types of gradients are likely to be commonplace over large portions of southern Asia, Africa and South America, where most of the urban growth is currently concentrated (Malakoff et al., 2016). In many of these regions, poor sanitary conditions in urban areas promote social acceptance of species that offer ecosystem services through refuse consumption, such as many scavengers (Bildstein & Therrien, 2018; Barlow & Fulford, 2013; Campbell, 2009; Gangoso et al., 2013). Because sanitary conditions are usually tied to poverty, which is typically heterogeneously distributed within cities (Kilroy, 2009), the stage is set for socially-generated variation in subsidies and resources, as well as human perceptions and responses to wildlife. Finally, the effect shown here of socio-cultural factors on wildlife populations implies that geographic variation in human cultural aspects can generate marked variation in the basic functioning of urban ecosystems from different regions. This stresses the urgency of completing our views of urban ecology through more studies on the strongly overlooked cities of the so-called developing world.

Implications for management and conservation

Interestingly, both the factors that seemed to limit the kite population (food and breeding-sites) were already directly or indirectly managed by humans. In particular, nest availability could easily be exploited through tree addition or removal in order to increase or constrain local predator density. For example, density could be enhanced close to urban areas with poor sanitation infrastructures in order to boost the ecosystem service function of kites, while density could be reduced in areas with conflictive pairs that attack humans for nest defence or to steal food (Kumar et al., 2019). Because urban ecosystems are typically temporally dynamic, a good understanding of the factors underlying local abundance is key to forecast or minimize the future impacts of such changes. For example, urban development in Delhi is currently causing rapid and often dramatic erosion of tree-cover (Paul & Nagendra, 2015). This could cause a progressive decline in the ecosystem service offered by kites, with potential repercussions even on human health, for example through an increase in rotting organic waste or in populations of feral dogs. The latter are a major source of rabies for humans in India and have been shown to increase in response to declines of scavenging birds (Markandya et al., 2008).

In conclusion, human socio-cultural factors may represent a widely overlooked force in urban ecology and conservation, and their impact may be even greater than currently appreciated in the poverty-structured cities of the developing world, where social inequalities and cultural beliefs may be tied to human subsidies and wildlife perceptions. The massive foodbase so generated may have population impacts further modulated by anthropogenic structures that provide safe breeding, roosting and resting sites, whose availability could be easily exploited as a management tool. Thus, for many urban animals key resources are inextricably linked to human culture.

Acknowledgements

We thank Ujjwal Kumar and the Director of the Wildlife Institute of India for materials and advice on various aspects of the project. We thank Laxmi Narayan, Prince Kumar, Poonam and all the "Black Kite Project Group" for help in the field.

References

- Alberti, M., Marzluff, J. M., Shulenberger, E., Bradley, G., Ryan, C., & Zumbrunnen, C. (2003). Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. *AIBS Bulletin*, 53(12), 1169-1179.
- Alberti, M. (2008). Advances in urban ecology: integrating humans and ecological processes in urban ecosystems (No. 574.5268 A4). New York: Springer.
- Barlow, C. R., & Fulford, T. (2013). Road counts of Hooded Vultures Necrosyrtes monachus over seven months in and around Banjul, coastal Gambia, in 2005. *Malimbus*, 35(1), 50-56.
- Bildstein, K. L., & Therrien, J. F. (2018). Urban Birds of Prey: A Lengthy History of Human-Raptor Cohabitation. In *Urban Raptors* (pp. 3-17). Island Press, Washington, DC.
- Boal, C. W., & Dykstra, C. R. (Eds.). (2018). Urban raptors: ecology and conservation of birds of prey in cities. Island Press.
- Campbell, M. (2009). Factors for the presence of avian scavengers in Accra and Kumasi, Ghana. *Area*, 41(3), 341-349.
- United Nations, Department of Economic and Social Affairs, Population Division (2014). *World Urbanization Prospects*: The 2011 Revision.
- Faeth, S. H., Warren, P. S., Shochat, E., & Marussich, W. A. (2005). Trophic dynamics in urban communities. *AIBS Bulletin*, 55(5), 399-407.
- Forman, R. T. (2014). Urban ecology: science of cities. Cambridge University Press.
- Francis, R. A., & Chadwick, M. A. (2012). What makes a species synurbic?. Applied Geography, 32(2), 514-521.
- Gangoso, L., Agudo, R., Anadón, J. D., de la Riva, M., Suleyman, A. S., Porter, R., & Donázar, J. A. (2013). Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem services providers. *Conservation Letters*, 6(3), 172-179.
- Gaston, K.J. editor. (2010). Urban ecology. Cambridge University Press, Cambridge, UK.

- Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global change and the ecology of cities. *science*, 319(5864), 756-760.
- Kilroy, A. (2009). Intra-Urban Spatial Inequality: Cities as" Urban Regions".
- Kinzig, A. P., Warren, P., Martin, C., Hope, D., & Katti, M. (2005). The effects of human socioeconomic status and cultural characteristics on urban patterns of biodiversity. *Ecology and Society*, 10(1).
- Kumar, N., Mohan, D., Jhala, Y. V., Qureshi, Q., & Sergio, F. (2014). Density, laying date, breeding success and diet of Black Kites Milvus migrans govinda in the city of Delhi (India). *Bird study*, 61(1), 1-8.
- Kumar, N., Gupta, U., Jhala, Y. V., Qureshi, Q., Gosler, A. G., & Sergio, F. (2018a). Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools. *Urban Ecosystems*, 21(2), 339-349.
- Kumar, N., Qureshi, Q., Jhala, Y. V., Gosler, A. G., & Sergio, F. (2018b). Offspring defense by an urban raptor responds to human subsidies and ritual animal-feeding practices. *PloS* one, 13(10), e0204549.
- Kumar, N., Jhala, Y.V., Qureshi, Q., Gosler, A.G., & Sergio, F. (2019). Human-attacks by an urban raptor are tied to human subsidies and religious practices. In press in: *Scientific Reports*.
- Magle, S. B., Hunt, V. M., Vernon, M., & Crooks, K. R. (2012). Urban wildlife research: past, present, and future. *Biological conservation*, *155*, 23-32.
- Malakoff, D., Wigginton, N. S., Fahrenkamp-Uppenbrink, J., & Wible, B. (2016). Rise of the urban planet. *Science*.
- Markandya, A., Taylor, T., Longo, A., Murty, M. N., Murty, S., & Dhavala, K. (2008). Counting the cost of vulture decline—an appraisal of the human health and other benefits of vultures in India. *Ecological economics*, 67(2), 194-204.
- Marzluff, J. M., Shulenberger, E., Endlicher, W., Alberti, M., Bradley, G., Ryan, C., ... & ZumBrunnen, C. (2008). An International Perspective on the Interaction Between Humans and Nature. Springer Science and Business Media, New York.

- Marzluff, J. M. (2017). A decadal review of urban ornithology and a prospectus for the future. *Ibis*, *159*(1), 1-13.
- McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. Bioscience 52: 883890 McKinney ML (2006) Urbanization as a major cause of biotic homogenization. *Biol Conserv*, 127, 247260.
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized linear mixed- effects models. *Methods in Ecology and Evolution*, 4(2), 133-142.
- Naoroji, R. (2006). Birds of prey of the Indian subcontinent. Christopher Helm.
- Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J., & Dickman, C. R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, 24(1), 1-11.
- Newton, I. (2013). Bird Populations (Collins New Naturalist Library, Book 124) (Vol. 124). HarperCollins UK.
- Newton, I. (1998). Population limitation in birds. Academic press.
- Newton, I. (1979). Population Ecology of raptors. t. & AD Poyser, london, U.K.
- Nimela, J., Breuste, J., Elmqvist,.... (Eds.). (2011), Urban ecology Patterns, processes, and applications, Oxford University Press, Oxford,UK.
- Oro, D., Genovart, M., Tavecchia, G., Fowler, M. S., & Martínez- Abraín, A. (2013). Ecological and evolutionary implications of food subsidies from humans. *Ecology letters*, 16(12), 1501-1514.
- Paul, S., & Nagendra, H. (2015). Vegetation change and fragmentation in the mega city of Delhi: Mapping 25 years of change. *Applied Geography*, 58, 153-166.
- Pinault, D. (2008). Raw meat skyward: pariah-kite rituals in Lahore. *Equinox Publishing*, 108-121.
- R Development Core Team. 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

- Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in ecology & evolution*, 21(4), 186-191.
- Taneja, A. V. (2015). Saintly animals: the shifting moral and ecological landscapes of North India. *Comparative Studies of South Asia, Africa and the Middle East*, *35*(2), 204-221.
- van Heezik, Y., Freeman, C., Porter, S., & Dickinson, K. J. (2013). Garden size, householder knowledge, and socio-economic status influence plant and bird diversity at the scale of individual gardens. *Ecosystems*, *16*(8), 1442-1454.
- van Heezik, Y., & Hight, S. R. (2017). Socio-economic-driven differences in bird-feeding practices exacerbate existing inequities in opportunities to see native birds in cities. *Journal of Urban Ecology*, *3*(1), jux011.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). GLM and GAM for count data. In *Mixed effects models and extensions in ecology with R* (pp. 209-243). Springer, New York, NY.
- Zuur, A. F., Ieno, E. N., & Saveliev, A. A. (2017). Beginner's guide to spatial, temporal, and spatial-temporal ecological data analysis with *R-INLA*.

kite breeding pairs within the city of Delhi (India). Variables were chosen on the basis of our knowledge of kite ecology and of previous 2018a,b, 2019). These variables characterized each plot in terms of its landscape structure, food availability (local availability of organic Table S1. Landscape and human variables used to characterize each study plot in which we surveyed the population density of Black analyses of the factors that affect habitat preferences, breeding success and behavioural performance by Delhi kites (Kumar et al. garbage, access to Muslim ritual-subsidies, local density of humans walking in the streets), and nest-site availability. See the Study Area section for background details on the rationale underlying the choice of indicators of human refuse and ritual subsidies.

Variable	Description
Nest-site	Density (number/km2) of structures potentially capable to support a kite nest, such as trees of sufficient height, or
availability	anthropogenic structures such as pylons and towers (Kumar et al. 2018a). For each plot, we: (1) digitized all large- enough trees clearly visible in Google Earth imagery; (2) visited each plot and mapped any additional trees that
	were not well visible in Google Earth (e.g. because of low quality, blurred imagery for some sectors of Delhi, or hecause of the shadow produced by tall buildings) and all notential anthronogenic nest-structures (e.g. poles, towers)
	that were typically too difficult to detect in Google Earth. For plots in which nesting-structures were too many to count individually. we: (1) plotted 20 random locations within each plot: (2) visited them in the field and counted
	all nesting-structures observed in a circular buffer of 200 m radius centered on each of these 20 random locations
	to calculate a cumulative density of nesting structures/km ² . Because more than 90 % of the available nest-structures
	were trees, we summed trees and artificial structures into a single cumulative estimate of breeding-site availability.
Refuse	Level of sanitation of the plot: 1 = clean areas (efficient waste disposal with very scarce or no organic refuse in the
availability score	streets); 2 = areas under poor waste management regime (abundant and widespread refuse in the streets throughout the area, either in small frequent piles, in illegal ephemeral dumps, or as individual items scattered a bit of
	everywhere through all streets).

Average number of people walking within 2m of a stationary observer during 5 min at 10 locations randomly plotted within 200 m of a nest, and averaged over all nests censused in a plot. Counts were only operated between 10:00-

Human density

17:00 hrs and avoided during atypical, momentary peak periods of human traffic, such as exits from work or schools, in order to maintain consistency across sites (following Kumar et al. 2018a).

- st, 2nd and 3rd nearest Muslim colony (see Kumar et al. 2018a for details). Thus, to provide a comprehensive the proximity of the plot to the three closest Muslim colonies. A key variable in our previous analyses on the predictors of kite site selection, occupancy, breeding and behavioral performance was the ease of access to dense More specifically, we previously showed that Delhi kites over-selected breeding sites closer than available to the measure that integrated the proximity to the three nearest Muslim colonies with their human population density (under the assumption that higher rates of refuse and ritualized-feeding should occur in more densely-populated Muslim colonies), we extracted the first axis (PC1) of a Principal Component Analysis (PCA) run on these four aforementioned variables. Its PC1 (hereafter "access to Muslim subsidies") explained 83% of the variance and had a high positive loading on Muslim population density and high negative loadings on the distance to the 1st, 2nd and 3rd closest Muslim colonies. Thus, it provided an increasing index of access to abundant "Muslim subsidies" (details First component (PC1) of a principal component analysis on the density of Muslim inhabitants in the plot and on Muslim colonies, which provide abundant food supplies in the form of ritual subsidies (Kumar et al. 2018a, b). in Kumar et al. 2018a). Muslim subsidies Access to
- Number of asphalted roads crossed by a 500 m north-south and a 500 m east-west transect crossing each other on a nest, and averaged over all nests censused in a plot. Index of road density

Appendix S1. Spatial analysis of Black kite density

Methods

Because of potential spatial dependency, kite density was initially modelled through a spatial linear mixed model (LMM) by means of Bayesian methods, as detailed in Zuur et al. (2017). The model incorporated a Guassian Markov random field that controls for spatial dependency and autocorrelation. The estimation of the spatial random field was based on the creation of a dense triangular grid (mesh) overlaid on the study area (Fig. 1 below) to solve a "continuous domain stochastic partial differential equation" (SPDE), in turn used to calculate the parameters of the Matérn correlation function which estimates the spatial random term. The explanatory variables (see Methods and Table S1) were fitted to the model through diffuse priors, and considered as "important" when their 25 % and 95 % credible intervals did not overlap zero. Study plot identity was always fitted as a random effect. Support for inclusion of a spatial random field was examined by comparing the LMM with and without the spatial field by means of the DIC statistic. Zuur et al. (2017) suggest a Δ DIC > 10 units to provide support for a model over another. All model building and checking procedures follow Zuur et al. (2017).



Fig. 1. Mesh overlaid on the Delhi study area to estimate the spatial field fitted to the linear mixed model used to relate kite density to explanatory variables. The mesh was based on a grid of > 4000 triangle-vertices (4299), following recommendations by Zuur et al. (2017). The black circles represent the kite study plots.

Results

Two variables appeared as important, as their 25 % and 95 % credible intervals did not overlap zero (see Table 1 below). These were: human density and the interaction between Access to Muslim subsidies and Nest availability. There was poor support for the need of a spatial random field: the spatial model was only 2.78 DIC units less than the model without a spatial random field.

Table 1. Slope and credible intervals of a spatial linear mixed model testing the effect of landscape structure, food availability and breeding-site availability on the population density of an urban raptor. Important variables, whose credible intervals do not overlap zero, are highlighted in bold.

Variable	Mean	25 % credible interval	95 % credible interval
Intercept	-15.33	-44.63	14.55
Access to Muslim subsidies	-3.40	-27.08	20.35
Quadratic effect of Access to Muslim subsidies	-6.84	-18.52	4.87
Nest availability	-0.01	-0.04	0.02
Hygiene score	-1.27	-4.53	1.96
Human density		3.76	32.23
Index of road density	1.04	-1.64	3.76
Access to Muslim subsidies * Hygiene score		-0.99	2.74
Access to Muslim subsidies * Nest availability		0.01	0.03
GPS-telemetry unveils the regular high-elevation crossing of the Himalayas by a soaring raptor: implications for definition of a "Central Asian Flyway"

*Unpublished, and under consideration for submission to a general ecological journal.

Additional research activities as a background support to Chapter 6

During the development of the thesis, I had occasion to participate to a paper that is directly related to this chapter and which assessed the potential impact of GPS-tagging on Black kites, using data from an intensive tracking-study on the Spanish population. I participated to the statistical analyses of this assessment, as part of my training into radio-tagging afforded by Dr. F. Sergio and his research group, and aimed at familiarizing myself with radio-tagging techniques and GPS-data processing in order to re-apply these techniques to my Delhi study population. The assessment led to a co-authored paper, titled, "*No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring*".

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Originally published on August 04, 2015; Volume 52, Journal of Applied Ecology

• <u>Published typesetting included in the Appendix</u>



Black-eared Kites *milvus migrans lineatus* over the Ghazipur landfill site in Delhi – (Ghaziabad highway) in the peak winter months. About 90% of the flock is constituted by the Black-eared Kites (pers. obs). Photo credit: Dr F Sergio

Abstract

Remote technologies are producing leapfrog advances in identifying migratory routes and the connectivity between breeding and non-breeding areas of migratory species, which are cornerstones to their conservation and management. However, these aspects are still completely unknown for hundreds of common taxa and especially so for Asian migrants, which have received very scanty tracking-research. Here, we used GPS-telemetry to uncover the unknown migration routes and breeding areas of the massive population of migratory Black-eared kites Milvus migrans lineatus which winter around the megacity of Delhi, thus contributing to generate the largest raptor concentration of the world. Kites migrated along a rather narrow corridor, almost invariably crossed the Himalaya at extremely high elevations (up to > 6000 m a.s.l.) through its western portion by the K2 of the Karakoram Range and spent large portions of their journey (up to > 500 km) at elevations above 3500 m. They then crossed or circumvented the Taklamakan Desert and the massive Tian Shan Range to reach their previously unknown breeding quarters at the intersection between, Russia, China and Mongolia. Route configuration seemed to respond to the interplay between dominant wind support and barrier avoidance, and negotiation of such major obstacles produced migratory performances comparable to those reported for easier routes. Individual- and population-level wintering ranges were concentrated around Delhi and were smaller than the breeding ranges, likely in response to the massive human waste provided intentionally and unintentionally by an extremely dense human population. Remote-tracking of this extremely common species suggests that high-elevation Himalaya crossing may be more common than previously appreciated. Based on this and previous studies, we suggest the delineation of a hitherto poorly appreciated "Central Asian Flyway", which must funnel hundreds of thousands of soaring and non-soaring migrants from central Asia into the Indian subcontinent via multiple modes of Himalaya crossing.

Synthesis

This dissertation is part of a larger and long-term study on the demography of Black Kite in Delhi. In the previous chapters, I have shown several ways in which kites have managed, at both the individual and population-level, to adapt to and exploit the urban environment provided by humans, together with its anthropogenic subsidies that offer a potential food bonanza to a facultative scavenger species like the Black Kite. Below, I offer a brief recapitulation of the main results of each chapter, I especially highlight the results that may be of interest to a broad audience rather than to a selected group of kite or raptor enthusiasts, and then proceed to expose the future research directions that will emanate from the results exposed in this thesis.

A cursory examination of the study population in 2013 corroborated and elucidated the previously established importance of extensive and predictable foraging opportunities for an urban population of a facultative scavenger, the Black Kite (Galushin, 1971; Malhotra, 2007). I started my doctoral dissertation after identifying the long-term stability of the breeding density of kites in Delhi since 1960–1970s (Kumar et al., 2014). This represents the highest ever reported breeding density estimate for a raptor of its size (Chapter 1). The availability of food is further complemented by a stable favourable climate which extends the time span for breeding, as reported for other avian populations exploiting urban food super-abundance. Smaller breeding raptors, such as falcons, usually respond by laying a larger clutch, and multiple broods. Urban kites, in comparison, have benefitted from the low density of potential predators in the city (Lin et al., 2015), a general absence of human persecution and a long history of religious tolerance towards living beings, which sustains wildlife and feral animals at extremely high densities within hundreds of South Asian megacities. Furthermore, while kites did not appear to face any conservation concern, recent urban development is causing widespread

removal of mature trees in many sectors of the city (Paul & Nagendra, 2015). Nest site availability is identified as one of the two pillars for raptor biology, the other being food (Newton, 1979). Because Delhi kites mainly nest on trees and use other structures (e.g. pylons or towers) only when trees are in scarce supply, tree availability could limit the kite population in the future, triggering local declines and re-distributions. In Chapter 5, I demonstrate the importance of nest availability at the population level. Thus, the ecological service provided by kites through removal of organic rubbish, the abundance of the species in Delhi, and the current low sanitary levels of the city can be seen as a template that supports the importance of the continued health and existence of this remarkable raptor concentration in such an urban environment. My preliminary work suggested the need for continued monitoring of this population and its urban nesting habitat in future years.

Research gaps on tropical megacities regarding the interplay between a top trophic predator's habitat selection and human socio-economic aspects were addressed in Chapter 2. Here, the research design examined how our model species exploited its supporting highly anthropogenic ecosystem. While modelling breeding habitat selection by a predator and facultative scavenger in a tropical megacity we took into consideration, the spatial associations that tie together human refuse and its prey-fauna, the ritualized feeding of kites (see detailed descriptions of ritualized feeding practices in Chapter 2, 3, 4 and 5), and habitable vegetation patches. The habitat decisions of kites responded in such a way as to optimize the opportunistic uptake of predictable foraging resources tightly enmeshed with human activities. I found that breeders preferred areas with high human density, with poor waste management, with a road configuration that facilitated better access to resources provided by humans and, in particular,

with ready access to Muslim colonies that provided ritual subsidies. Analysis of the relationship between the same variables and breeding success further confirmed the importance of access to human ritual subsidies. Our results stress the importance of human activities, even politics, history, socio-economics and urban planning at multiple spatio-temporal scales (Chapter 2 and 5) when studying the distribution and habitat associations of predatory and scavenging species within highly anthropogenic ecosystems.

After examining the general status, breeding ecology and habitat choices that allowed kites to cope with a highly anthropogenic environment, I investigated some behavioural aspects that may on one hand be adaptive (in terms of offspring defense against enemies) but on the other create potential conflicts with humans. The analyzed behaviour was the defence of eggs and nestlings by parental kites, which showed how kites were able to subtly discriminate how to act in the presence of people feeding them and in the presence of people approaching their nest and thus representing a potential danger. Thus, in Chapter 3, I elucidated the decision of parent birds to indulge in an aggressive response to human intruders. Here, humans (research team) were a surrogate to test variations in parental investment to imminent threats by potential nest predators. The analysis also explored the fitness consequences of investment in aggressive defense by parent birds. I found that the intensity of nest defense was associated with larger broods, it increased with the progression of the breeding season and was once again related to human socio-religious variables that set the scenario of food availability and territory quality for individual kites, thus impinging on their prospects for breeding success, their parental investment and defense motivation.

In Chapter 4, I "zoomed-in" on an aspect of nest defense that may represent a potential challenge and cost for kites' ability to persist in a city, namely their frequent attacks on humans during nest defense. In this context, I hypothesized once again that the both ecological and human factors, and especially the latter, could enter the dynamics of human-aggression by kites. Results of this analysis showed that the likelihood of attack responded to human activities and practices, such as unhygienic waste management, ritual-feeding of kites, human density, and urban architecture in the nest-surroundings (the presence of a balcony) that increased the frequency with which kites were exposed to humans, thus contributing to lower their fear. While many behavioural studies have suggested an association between aggression and frequent-close exposure to humans to derive food-rewards, few studies have focused on the potential mechanisms that may generate aggression. Surprisingly, while most people living near nesting kite territories acknowledged the risk of attack in any given moment, their attitudes were strikingly sympathetic towards the birds, even by injured people, likely as a result of religious empathy. This "fragile urban amiability" at the human-animal interface was based on two different trade-off decision paths: first, originating from the kites' end as they capitalise on anthropogenic foraging benefits, and **the second** from the people' end whose accommodative attitude allowed for the proximity of aggressive animals. From the responses of our interviewees, this attitude appeared to be driven by religious reverence and a recognition of the ecosystem service (refuse removal) provided by the aggression-culprits. These results highlight the importance of socio-cultural factors for urban biota and how these may radically differentiate the under-studied cities of developing countries from those of western nations, thus broadening our picture of human-wildlife interactions in urban environments. I believe that similar dynamics will soon be observed in other cities of the developing and developed world,

as rapid sprawling of urban and suburban areas with their associated food-subsidies is likely to increase proximity and exposure of large predators to humans, and vice versa, leading to heightened worldwide conflicts.

Human socio-cultural factors have been recognized as fundamental drivers of urban ecological processes. But their population-effects on urban wildlife are still poorly known. In the Fifth Chapter, I explored the relationship between human cultural aspects and Black Kite population-level densities and find a tight relationship. I argue that these sorts of relationships are likely to be stronger in tropical cities than in the more extensively studied but very different settings of temperate cities. Our models offer explanations for profoundly different niches for urban wildlife. In particular, I examined how kite populations can capitalize on spatial variation in human subsidies, mainly in the form of philanthropic offerings of meat given for religious purposes. I further argue that this tight connection with human culture has generated the largest raptor concentration in the world, with its spatial variations being further modulated by breeding-site availability. This further supports the qualitative arguments presented in Chapter 1 on the importance of breeding site availability for population limitation. As the limiting factor for urban ecosystems, the availability of trees constrained the level of resource-tracking by the kites and their potential to provide an 'ecosystem service'. I thus proposed to employ tree management as a potential tool to manipulate kite density (e.g. in the case of aggressive humankite interactions). A major implication of these results is in managing many urban animals whose key resources are inextricably linked with human culture.

Furthermore, exploration of the possible future scenarios pertaining to the aggressive human-kite interface seems necessary in the context of a rapidly expanding megacity. Understanding such conflicts in detail requires an interdisciplinary approach, combining ecology, ethology and the social sciences, beyond the current scope of this thesis. In addition, it will also need an approach spanning multiple scales of analysis, examining relations that are manifested locally at a nest/breeding territory scale, to the ones that pan out at a landscape level. Drawing this further from the discussions within Chapters 2, 3 and 4, aggressive interactions and boldness to human presence are known to pose a nuisance to humans, moderated by the current cultural geography based on religious reverence for animals. However, quite often, a society's ways to express its identity results in associations with candidate animals, for e.g. dogs and monkeys. This argument could not be timelier, given recent drives to incorporate "smart city" outlooks i.e. modern infrastructure within large tropical cities, and the socio-cultural and political dialogue modulating State and Citizens' expression toward specific 'holy' animals, such as cows, monkeys. In the absence of an active state-based intervention to popularize or celebrate the religio- cultural ties with commensals like kites, the "progressive", younger generations already seem less interested in cultural practices such as ritualized-feeding. I predict that future 'decoupling' of cultural-ecological ties in people and kites would impact in unforeseen ways, much in the line of the Red Kite's fate in the city of London (see below), where progressive improvement of city infrastructure turned kites from 'useful' city scavengers to nuisance animals. In the context of the latter, I also predict the "catalytic effect" of aggressive interactions in humans and kites in the coming decades, towards 'decoupling' of culturalecological ties in people and kites. I recommend using anti-bird spikes to deter aggressive kite pairs from nesting very close to a human locality. Such interventions should be coupled with

harnessing the scavenging ecosystem-service of kites in the nearby informal settlements plagued with solid waste issues (see below). These must go hand-in-hand with the Government's periodic attempts to 'improve' and relocate informal settlements, abattoirs, and landfill sites which impact scavengers like kites.

The destruction of informal settlements, as a way of slum "rehabilitation", can disrupt the human-waste-commensal relationship within a local system, forcing the dispersal of coexisting commensals (as aggressive pairs, or as reservoirs and vectors of zoonoses) to surrounding areas, in response to the sudden absence of 'predictable' refuse and ritual subsides. Data on kite densities, amount and types of waste, and their spatial distribution should be used to test the prediction of higher prevalence of aggressive human kite interactions in the surrounding areas of a slum rehabilitation site. Through the fieldwork, I found that, while food subsidies are a common phenomenon within the city, the inhabitants of affluent 'centres' tend to dislike the constant presence of animals, excreta, or their aggressive behaviour. Following this doctoral research, I explain below, the use of observational, ethnographic and instrumentation aspects which can enhance extensions of this research in monitoring slums rehabilitation and relocation/culling of 'problematic' commensals e.g. kites, monkeys and dogs. Incorporation of empirical and site-specific urban ecological models in estimating the conflict threats by a particular commensal will help to minimize conflict and promote the ecosystem services such animals offer in developing megacities. This thesis proposes indicative mechanisms, whose extension in the form of long term studies on commensals shall aid in opting socially and scientifically informed steps to control, cull or translocate animals.

A comprehensive research project which factored the constituency of human refuse in the diet of an avian scavenger warrants some light on the outputs of the purported ecosystem services provided by the kites. As outlined in Chapter 4 and 5, I calculated a preliminary rough estimate of the annual ecosystem and sanitary services offered by these city scavengers (as tones of organic waste removed by the cumulative population). Kites' direct ecosystem service can be translated in terms of safe disposal of the organic waste, which could otherwise decay and lead to disease outbreaks. This estimate also has likely implications for public health security, which might be quantified in terms of mitigation of zoonotic threats caused by the competitive release of mammalian scavengers within the city, such as feral and stray dogs and rodents. Markandeya et al. (2008) discussed the effect of the competitive release of feral dogs as an outcome of a catastrophic decline of vultures, an argument which I would fully extend to the ecosystem services of the kites, especially in poverty stricken areas, i.e. the informal settlements which suffer from issues of solid waste management. Elaborating on Chapter 5, the incidence of zoonoses like rabies and leptospirosis could be mitigated by quick "crane-assisted tree plantation" near the areas marred by physical and zoonotic conflicts by the non-avian scavengers. Such trees can be used as nesting substrates/communal sites by the resident and migratory populations of kites. With no prior quantitative records of commensals within local city sub-systems, these interventions also need to factor the changes in animal densities as case studies. However, I also suggest the need to evaluate harnessing of scavenging service by identifying trade-offs between waste-disposal benefits and zoonotic-threats carried by kites themselves to densely-populated areas.

No discussion on kites in India can be complete without studying the mega-flocks of wintering Black-eared kites in Delhi and other Indian megacities. In Chapter 6, I propose that many of the recent and historical reports of large or enormous flocks of kites associated with rubbish dumps were likely misidentified as kites of the *M. m. govinda* subspecies. In reality, the Indian subcontinent is an important wintering area for kites of the M. m. lineatus subspecies (Black-eared Kite), which breeds in central Asia and uses a network of Indian cities to overwinter. While the fact that Black-eared kites are migrants from central-northern Asia was already known and hypothesized, the frequent difficulty of quickly separating the two subspecies, which extensively overlap in the winter, has muddled knowledge about the extent of its contribution to the enormous kite concentrations observed in cities like Delhi. Furthermore, the migration routes and exact breeding ranges of these Delhi migrants were completely unknown up to now. Thus, to fill this gap of knowledge, I GPS-tagged 19 Blackeared kites and remotely followed their meanderings. The GPS-data showed that the individual and population-level ranges during winter were significantly smaller than the summering ranges, likely due to the massive availability of food, intentionally and unintentionally generated by human subsidies in the Delhi region. As urban and peri-urban landscapes also feature as wintering destinations for waterfowl and several other human commensals, telemetry research on common species such as kites highlights the importance of studies on the species using the Central Asian flyway, and its effect on urban residency and foraging.

Limitations

Possible Methodological Limitations

As explained in the discussion-section of Chapter 1, the reported frequency of the food remains collected inside and under the nest was strongly dominated by scavenged meat scraps, both by mass and number. We did consider this as a cursory assessment. To address the possibility of biases in the cursory approaches to diet analysis, we started deploying trail cameras at nests selected at random, within as many plots as possible. This methodological intervention of following breeding events at 40 nests through 2015-2018 found significant increase in the estimated frequency of scavenged meat scraps delivered by the parent kites (Chapter 5). Further, we aim to monitor about 25 nests every year using camera-trapping devices (model Reconvx Hyperfire), covering again the whole urbanization gradient and including most of the nests which are simultaneously and repeatedly sampled to assess the nestlings' growth rates. It should also be noted that an urban research system severely limits the opportunities of camera placement at a nest, because of the risk of theft of expensive equipment, and local concerns about surveillance. Furthermore, many nests do not have accessible branches to fix the camera, and in Delhi we are not in a position to use power tools as the latter attracts undue attention. Even data collected by a 24 X 7 camera installation at a large number of nests would still carry a bias in terms of the meat brought by the parent birds which never reaches the nest and is consumed by the either, out of the nest. To address this bias in light of estimating the "scavenging ecosystem service by kites", I will be using the tri-axial accelerometry data of modern GPS Platform terminal transmitters (see below). Given that the typical, perched style of feeding by a raptor will be quickly captured by the accelerometry data, I aim to calibrate these instances of foraging by parents away from the nest, to largely address the "holes" of scavenging ecosystem service not captured by the trail cameras. This calibration can easily differentiate whether or not a parent bird is feeding on a meat chunk/whole bodied prey. Alongside, I also intend to do ground-truth of the tri-axial accelerometry data to calibrate the data analysis software for specific foraging events.

<u>Possible Logistic Limitations in estimates of population numbers and stability of</u>

On the hindsight, I would stress on the discussion of population numbers and stability of breeding density of kites over the five decades of observation. In chapters 1, 2 and 5, I reported the comparison of only landscape-based estimates of kite density within the capital with the estimates provided by previous studies, all of them conducted in the 1970s. These previous studies(e.g. Galuhin 1971), unfortunately, were not reported with sufficient detail to enable a quantitative comparison, except the reports of number of nesting territories within the National Zoological Park (Chapter 1) by Malhotra (2007). Therefore, my inferences about the stability in density (Chapter 1 and 5) should be taken with caution. Furthermore, the preliminary rationale of establishing the Black Kite Project was to understand the impact of the local loss of vultures on the breeding density of kites. Although I found no significant change in the density estimates, using it as plain-speak "stability in density" over the five decades might be misleading, given the high variance around the mean that I found (Chapter 1). These values should rather be interpreted as qualitative proof of the opportunistic resilience of kites within an urban system, city scavengers which keenly-target foraging resources linked to human activities, politics, history, socio-economics and urban planning at multiple spatio-temporal scales. Finally, continued monitoring of the population in the decades to come will give us the unique opportunity to see how the population of this predator will respond to the future changes

that will surely affect a rapidly modernizing, expanding and ever-evolving megacity such as Delhi.

Conclusion

Over the long-term, Delhi and other rapidly-developing tropical megacities are likely to repeat the past and current development trajectories of western megacities like London (Grossman & Hamlet, 1964). Their rapid socio-economic development in coming decades will largely manifest in terms of changes in internal structure, management and culture, with expectedly marked improvements in sanitary infrastructures and refuse disposal. Like the fate of their congeneric Red Kite Milvus milvus in old London, infrastructural developments, economic change, and the already visible cultural shifts in younger generations will imply major alterations in resource availability and predictability for many synurbic species (Francis & Chadwick, 2012; Hulme-Beaman et al., 2016). Such unique systems of human-animal coexistence and its impeding conundrums caused by modernization will bring formidable challenges to urban societies. The results of this thesis suggest that, after centuries of urban colonization and of co-existence by kites with humans, their ecology and behaviour is finely tuned on spatial variation in human religion, hygiene and poverty. Further research is needed on synurbic animals in their mature stage of adaptation to an urban life, to understand the finegrained adjustments to urban structure and human culture, and to model the up-scaling of individual processes to population-level patterns.

Setting a long-term vision

Over the six years of monitoring at 28 independent sampling plots (complemented by longitudinal monitoring of a subset of 11 plots), I have completed a preliminary data collection of multiple behavioural, life history, and population parameters (e.g. clutch size, brood reduction, nestlings' growth) of the kites, collected all along the urban gradients of Delhi. Time has prevented inclusion of all the collected material into the current thesis, and I have preferred to examine in detail some aspects that particularly fascinated me (e.g. human attacks, relation with human cultural subsidies, migration) leaving so many other, equally interesting aspects for future investigation.

These will receive proper attention in due time, as I plan to continue my (hopefully long) research career developing several further subject that will allow me to disentangle the many facets that compose the overall picture of how kites manage to respond, adapt and exploit humans and their anthropogenic main medium, i.e. cities. In brief, main candidates for my future research will be the placement of camera-traps in nests to assess how diet composition and parental provisioning affect the growth rates, health status and stress levels of nestlings, and how all these parameters are in turn affected by urban, ecological and human socio-cultural factors. This will allow me to explore further mechanistic links that may mediate kites' capabilities of exploiting the urban medium.

A further aspect that is dire need of knowledge is the movement ecology of the resident *govinda* kites and how foraging behaviour responds in detail to the complex environment provided by the city and by its system of frequent but short-lasting and ephemeral episodes of ritualized feeding. Obvious questions regarding such aspects include: how far do individual kites travel to exploit ritualized feeding episodes? How do they detect them? Do some

individuals specialize to attend certain places at specific hours so as to capitalize on more predictable feeding events? Do kites nest more densely close to Muslim colonies so as to better locate ritualize feeding episodes through social facilitation (e.g. by observing the sudden departure of close neighbours)? The rapid miniaturization of GPS-devices will soon enough enable us to tag *govinda* kites in efficient manners in order to set-up ad hoc experiments and intensive monitoring to test such ideas.

In conclusion, the material exposed in this thesis is but the start of an intensive study that I set-up and started during my Master studies and that quickly converted into a long-term endeavour. The chapters here presented should thus be considered as an initial assessment, by necessity incomplete, which will be broadened, enriched and refined over the coming years.

References

- Francis, R. A., & Chadwick, M. A. (2012). What makes a species synurbic?. Applied Geography, 32(2), 514-521.
- Galushin, V. M. (1971). A huge urban population of birds of prey in Delhi India. *Ibis*, *113*(4), 522-522.
- Grossman, M. L., & Hamlet, J. N. (1964). Birds of prey of the world. Crown.
- Hulme-Beaman, A., Dobney, K., Cucchi, T., & Searle, J. B. (2016). An ecological and evolutionary framework for commensalism in anthropogenic environments. *Trends in* ecology & evolution, 31(8), 633-645
- Kumar, N., Mohan, D., Jhala, Y. V., Qureshi, Q., & Sergio, F. (2014). Density, laying date, breeding success and diet of Black Kites Milvus migrans govinda in the city of Delhi (India). *Bird study*, 61(1), 1-8.
- Lin, W. L., Lin, S. M., Lin, J. W., Wang, Y., & Tseng, H. Y. (2015). Breeding performance of Crested Goshawk Accipiter trivirgatus in urban and rural environments of Taiwan. *Bird study*, 62(2), 177-184.
- Malhotra, A.K. (2007). Tiger of sky-Pariah Kite, PhD thesis, Shilalekh Publishers, Delhi.
- Markandeya, A., Taylor, T., Longo, A., Murty M.N., Murty S., Dhavala K. (2008). Counting the Cost of Vulture Declines Economic Appraisal of the Benefits of the Gyps Vulture in India. *Ecological Economics*, *67*(2), 194-204.
- Newton I. (1979). Population ecology of raptors. Poyser, Berkhamsted, UK.
- Paul, S., & Nagendra, H. (2015). Vegetation change and fragmentation in the mega city of Delhi: Mapping 25 years of change. *Applied Geography*, 58, 153-166.



Research team explaining scientific objectives and informing citizens of Delhi on the ecological importance of predatory kites (as well as other birds) while ringing kite chicks. This sort of citizen-group assembles constantly in a megacity of more than 16 million inhabitants like Delhi, as we move from nest to nest during our routine fieldwork activities, offering a unique opportunity to reach thousands of people in disseminating science, and educating the population on urban environmental issues of conservation importance. Since 2013, we have reached more than 50,000 citizens through this mobile conservation education initiative, which we see as a mobile laboratory. For many of these people, this may be one of their few opportunities to empathize and get in contact with nature, but our conversations with people have often surprised us by the depth of concern that they already have, for example for the decline in numbers of small birds that they have noticed over recent years.

Appendix

[Typescript Journal Articles (6) and two Comic Booklets in English and Hindi]

ISSN: 0006-3657

Volume 61, Part 1, February 2014

Bird Study The Science of Pure and Applied Ornithology







Density, laying date, breeding success and diet of Black Kites Milvus migrans govinda in the city of Delhi (India)

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Capsule The density of Black Kites in Delhi, India, may represent the highest concentration of a raptor recorded in the world and has not declined since the 1960s.

Aims To estimate the density, phenology, breeding success and diet of Black Kites in Delhi.

Methods During 2013, Black Kite nests were surveyed in 24 plots of 1 km² distributed throughout Delhi. A sample of 151 nests was checked regularly to record laying date, breeding success and diet.

Results The average density was 15 nests/km². The majority of nests were on trees (91%) and the rest on artificial structures. Mean laying date was 31 January and the laying season was protracted over four months. Mean number of fledged young was 0.73, 1.09 and 1.53 per territorial, breeding and successful pair. Diet was dominated by scavenged meat and by rats, pigeons and doves abundant in the city. **Conclusions** Density has been stable since 1960–1970s and probably represents the highest ever recorded for a raptor. This is probably promoted by a combination of (i) availability of rubbish, (ii) few predators and (iii) high tolerance by people. The conservation status of this raptor seems satisfactory, but removal of mature trees for rapid development may result in local declines or re-distributions, suggesting the need for continued monitoring.

The Black Kite *Milvus migrans* is a medium-sized raptor, currently considered as one of the most numerous and successful birds of prey of the world (Ferguson-Lees & Christie 2001). It is a generalist, opportunistic feeder, capable of reaching extremely high densities where food concentrations allow it (e.g. review in Sergio *et al.* 2005, Malhotra 2007) and may occupy habitats which range from fully natural to completely urban (Ortlieb 1998, Ferguson-Lees & Christie 2001). Such opportunism and capability to exploit human-modified habitats has afforded this species a generally favourable conservation status, with frequent reports of recently increasing populations, despite some local declines (Bijlsma 1997, Sergio *et al.* 2003, Thiollay & Bretagnolle 2004).

This capability to adapt to human landscapes reaches its extreme in populations that nest in fully urban conditions, as frequently observed in Asia and Africa (Desai & Malhotra 1979, Brown et al. 1982, Ali & Ripley 1983, Naoroji 2006). In these settings, kites are reported to use the urban ecosystem not only for nesting but also for feeding on human offal, road kills, animal carcasses and rubbish, sometimes forming spectacular concentrations of thousands of individuals at rubbish dumps of large cities (Brown et al. 1982, Owino et al. 2004, Naoroji 2006, Malhotra 2007). When these dumps are located in the proximity of airports, the concentration of kites often generates serious management problems because of the risk of collisions with planes (Satheesan 1996, Owino et al. 2004). It is remarkable that, despite their overall abundance and frequent proximity to humans, Black Kites have been very rarely studied, except for two or three intensively investigated populations, all of them located in Europe and in non-urban settings (Viñuela et al. 1994, Blanco 1997, Sergio et al. 2003, 2011).

In the Indian subcontinent, where we conducted our research, the *govinda* sub-species is well distributed with dense populations in all the major urban centres (Naoroji 2006), which has attracted many anecdotal observations, as reported in several issues of the *Journal*

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of the Bombay Natural History Society (Hanxwell 1892, Fischer 1906, Ali 1926, Abdulali 1968, 1972, Mahabal & Bastawade 1985, Malhotra 1991). However, quantitative data for this biogeographic region are extremely scarce and previous studies, all of them conducted in the 1970s, have focused on: (1) a coarse estimation of the size of the overall Delhi population (Galushin 1971) and (2) data on the breeding ecology of the high-density colony of the Delhi Zoo (Desai & Malhotra 1979). Here, we report comprehensive quantitative data on the density, nest spacing, phenology, breeding success and diet of a fully urban population located within Delhi, India. We then compare the current estimates with historical records and with studies on other kite sub-species.

METHODS

Study area

Black Kites were surveyed in 2013 in 24 plots (details below) within an overall area of 1500 km² pertaining to the city of Delhi, India. Delhi is a mega-city of 16 million inhabitants in constant, rapid expansion (Census Organization of India 2011). The overall city comprises both urban and semi-urban areas under poor solid waste management, which affords plenty of food to Black Kites in the form of rubbish, carrion and remains from slaughterhouses. The climate is semi-arid, 64 cm of annual precipitation, with mainly concentrated in July and August. Temperature ranges from a mean maximum of 39.6°C to a minimum of less than 8.2°C in the winter (India Meteorological Department 2013). The vegetation of the general region falls within the 'northern tropical thorn forest' category (Champion & Seth 1968).

Field procedures

Because many areas of the city were private properties not accessible to the public, it was impossible to design a very large continuous study area. Also, because Black Kites in our area can attain extremely high densities, small-sized plots distributed over a wide area were judged to be better suited to sample all available conditions than a single continuous plot of necessarily limited extent. Therefore, we designed a network of 24 sample plots, each one of approximately 1 km² of homogenous accessibility and distributed throughout the city covering all types of potential nesting habitats. However, a standardized shape or a standardized surface of 1 km² could not be attained for all plots because of constraints imposed by private properties and logistical difficulties of access. Private properties had similar landscape features to the surrounding areas of the city and we are confident that their exclusion did not bias our density estimates. However, because of the above, nests which were located at the periphery of each sample plot were not employed to generate estimates of nest spacing (nearest neighbour distance henceforth referred as NND), unless a complete nest census had been conducted also for the area bordering the quadrat.

We surveyed each quadrat repeatedly every few weeks, starting from the pre-incubation period, by walking slowly and carefully inspecting all potential nest structures (trees, buildings, towers, etc.). Structures were classified as active nests when a kite individual or pair was repeatedly observed to perch in the nest or its immediate surroundings, or to add material to the nest. Once found, nests were checked by climbing to them, observing them from nearby vantage points, or through an eight-meter telescopic rod equipped with a videorecording camera. Nests were checked approximately every eight days. However, because of time, safety, accessibility and manpower limitations, data on breeding success were collected only at a sub-sample of nests.

A nest was classified as depredated when we found remains of plucked chicks. Cases of brood reduction (death of one chick, often caused by its siblings, subsequently fed to other nestlings) were not classified as predation events. Hatching date was calculated by backdating from the feather development of nestlings first observed when <15 day old and by comparison to reference information in Desai & Malhotra (1977), Cramp & Simmons (1980), Hiraldo et al. (1990) and personal data by one of the authors (F.S.). Laying date was estimated by subtracting 30 day, the average incubation period (Viñuela 1997), from hatching date. During each visit, we collected prey remains found inside and under nests and identified them to the genus or species level assuming the smallest possible number of individuals. These items were used to estimate each prey percentage contribution by number or by mass to the diet of Black Kites.

Terminology follows Steenhof (1987): a territorial pair was one that built a nest and then did or did not lay a clutch; a breeding or reproductive pair was one which laid eggs; a successful pair was one which raised at least one nestling until it was 40 day old; and breeding success was the percentage of successful territorial pairs. There was no need to correct the estimates of breeding success through Mayfield estimators, because all plots were surveyed repeatedly from the pre-laying period onwards, and because nests were easy to find and were checked very frequently (approximately every eight days). Density was calculated as number of territorial pairs per unit area and expressed as number of pairs/km². The difference in breeding success between nests located in trees and nests built on artificial structures was tested by means of a Z-test (Zar 1984). Throughout, means are given ±1 se, tests are two-tailed, and statistical significance was set at $\alpha \leq 0.05$.

RESULTS

Cumulatively, we censused 244 Black Kite nests in 2013. Out of these, 223 (91.4%) were located on trees and the rest on artificial structures (17 on electricity pylons and 4 on telephone metal towers). Out of 223 tree nests, 35.5% were built on *Eucalyptus* spp., 23% on *Ficus* spp., 13.8% on Neem (*Azadiracta indica*), 12.7% on Jamun (*Syzygium cumini*) and 8.3% on Keekar (*Prosopis juliflora*). The mean nest density was 15.1 ± 7.9 pairs/km² and varied between 0 and 67.1 nests/km² (n = 24 plots). Mean NND for the whole population was 133 ± 15 m and ranged between 5 and 2315 m (n = 207 pairs).

A subset of 151 nests was closely monitored for breeding success. The overall mean laying date was 31 January (n = 65, se = 3.3 days; range 19 December-13 April) and the laying season lasted almost 4 months (115 days), with a pronounced peak between the second half of January and first half of February (Fig. 1). When mean monthly temperature and rainfall were super-imposed on the laying frequency (Fig. 2), kites seemed to concentrate clutch initiation before the temperatures became excessively high and before the start of the Monsoon rains in June-July. The percentage of clutches initiated each month was negatively related to the minimum monthly temperature (linear regression: $B = -1.37 \pm 0.35$; B for constant = 34.21 ± 7.14 ; n = 12; Bonferroni-corrected P = 0.006; $R^2 = 0.56$) and quadratically related to the maximum monthly temperature (quadratic regression: B for linear term = -11.86 ± 3.66 ; Bonferroni-corrected P = 0.02; B for quadratic term: =0.17 ± 0.06; Bonferroni-corrected P = 0.02; B for constant = 211.37 \pm 54.04; n = 12; $R^2 = 0.77$), while egg laying stopped with the commencement of the rains and was initiated again only after the monsoon season. Finally, the



Figure 1. Temporal frequency of laying dates in the Black Kite population of Delhi (India) in 2013 (n = 65).

number of young fledged by each pair declined with laying date (linear regression: $B = -0.13 \pm 0.03$; *B* for constant = 1.66 ± 1.77 ; *n* = 65, *P* = 0.001; $R^2 = 0.17$).

Mean clutch size was 2.09 ± 0.06 (*n* = 100). Mean hatching success was $64.6 \pm 4.65\%$ (n = 72 nests). Of 137 chicks first observed when less than five days old, three were depredated (all from a single nest) and six were subsequently observed dead in the nest or simply disappeared, probably because of sibling aggression (Viñuela 2000). The mean percentage of nestlings lost by brood reduction was 0.16 ± 0.04 per brood (n = 91nests). The mean number of fledged young was $0.73 \pm$ 0.07 per territorial pair (n = 151), 1.09 ± 0.06 per breeding pair (n = 100) and 1.53 ± 0.04 per successful pair (n = 72). Forty-eight per cent of territorial pairs successfully raised their nestlings to fledging age (n =151). There was a trend for breeding success to be higher for nests on trees than for nest on the artificial structures (46% vs. 27.8%; Z = 1.8, P = 0.07, n for tree nests = 130, n for artificial substrate = 21).

Black Kite diet included all vertebrate classes but was strongly dominated, both by mass and number, by three main items: (1) remains from slaughterhouses, mainly in the form of compact chunks of meat; (2) rats and (3) medium-sized urban birds, such as doves and pigeons (Table 1).

DISCUSSION

Our study confirmed that Black Kites maintained extremely high breeding densities throughout the city of Delhi, as already observed in the 1970s (Galushin 1971). When compared with data from other populations (reviewed in Table 2), the density observed in the urban environment of Delhi was



Figure 2. Mean temperature, monthly rainfall and Black Kite laying frequency in Delhi (weather data from India Meteorological Department 2013).

Table 1. Diet of breeding Black Kites in Delhi, India (2012–2013), as
estimated by food remains collected inside and under the nest.

Prey category	Frequency by number (%)	Frequency by mass (%)	
Fish ^a	0.8	1.0	
Amphibians ^b	0.7	0.7	
Reptiles ^c	0.7	0.3	
Birds	24.6	31.9	
(i) Rock Pigeon (Columba livia)	13.1	16.2	
(ii) Collared Dove (Streptopelia	4.1	3.3	
decaocto)			
(iii) Other birds ^d	7.4	12.4	
Mammals ^e	9.8	20.2	
Scavenged meat ^f	63.4	45.9	
(i) Meat scraps	47.1	35.6	
(ii) Domestic chicken	11.5	6.1	
(iii) Cattle ^g	4.1	3.5	
(iv) Fish ^h	0.7	0.7	

^aUnidentified fish (n = 1).

^bIndian bull-frog (n = 1).

^cCommon house gecko (n = 1).

^dMoorhen (Gallinula chloropus) (n = 1), Indian Roller (Coracias

benghalensis) (n = 1), Unidentified birds (n = 7).

^eMammals which were unlikely to be consumed as carrion. Includes: Norway rat (*Rattus norvegicus*) (n = 11) and Palm squirrel (*Funambulus pennantii*) (n = 1).

¹Prey items that were considered to have been collected as carrion from local rubbish dumps and slaughterhouses.

^gBuffalo (n = 2), Goat (n = 3).

^hLarge unidentified fish skin, likely from fish market.

higher than any previously published estimate. This is then, probably, the highest density ever recorded over a large, continuous area for any bird of prey of this size. The capability to attain such a high population-level over such a large region is likely to be promoted by a combination of at least three factors. (1) First, the rubbish management plans of such a rapidly developing mega-city are inevitably poor, which results in a network of enormous, legally authorized rubbish dumps coupled with hundreds of smaller, and often illegal sites where garbage is dumped daily. At an even finer-scale, private individuals, families and shops often leave their daily garbage directly in the streets, resulting in a network of ephemeral, small piles of food. In turn, these must promote large populations of potential prey species, such as rats and pigeons. All the above, coupled with the high abundance of meat and fish shops throughout the city, sets an ideal scenario of enormous food availability for an opportunistic predator and facultative scavenger. (2) Second, the attitudes of local people towards kites, and wildlife in general, are extremely positive and tolerant, even despite the fact that some kites can be very aggressive in defending their nest against nearby passers-by. We are not aware of any cases of persecution of kites in Delhi, which is confirmed by the relative absence of

		Density	NDD in
Area (period)	Habitat	(pr/10 km ²) (n)	meters (n)
Delhi, India (2013) ¹⁷	U	150 (244)	133 (207)
Delhi, India (1967–1969) ³	U	161 (~560)	_
NZP, India (1979) ¹⁶	U	250 (18-21)	_
NZP, India (2013) ¹⁷	U	264 (70)	_
Matas Gordas, Spain (1987–1989) ¹⁰	м	70–150 (21– 45)	-
Matas Gordas, Spain (1992–2000) ¹⁵	м	100.8 (515)	-
Doñana, Spain (1981–1984) ⁸	м	26.7 (80)	206 (47) ^a
RBD, Spain (1989–2000) ¹⁵	м	15.1 (1059)	_
Lac Leman, Switzerland (1975– 1990) ¹¹	F	10.1 (319)	-
Neuchatel, Switzerland (1968) ⁵	FL	7.1 (337)	-
Lorraine, France (1966) ¹	WP	4.5 (66)	-
Rhône Plain, France (1970) ⁵	RP	60.9 (140)	-
Limousin, France (1976–1978) ⁴	PW	1.0 (21)	-
Lake Lugano, Italy (1992–1996) ¹³	WL	2.4–3.8 (27–	441
		41)	(175)
Lake Lugano, Italy (1992–2003) ¹⁵	WL	2.9 (365)	-
Lake Maggiore, Italy (1996–2000) ¹⁴	WL	-(24)	-
Lake Como, Italy (1996–2000) ¹⁴	WL	4.7 (40)	-
Lake Iseo, Italy (1996–2000) ¹⁴	WL	3.5 (48)	-
Lake Idro, Italy (1997–2001) ¹⁴	WL	6.7 (37)	-
Lake Garda, Italy (1997–2000) ¹⁴	WL	1.5 (18)	-
Sarca Valley, Italy (1997–2003) ¹⁴	WL	1.3 (88)	-
Castelporziano, Italy (1991–1992) ⁹	WF	3.3 (16)	103 (16) ^b
Monti della Tolfa, Italy (1973–1980)'	WP	0.5 (42)	-
Constance Lake, Germany (1968– 1969) ²	FL	1.9–2.2 (25– 30)	-
Drömling, Germany (1993–1994) ¹²	F	0.7 (8)	2330 (8) ^c
Brandenburg, Germany (1979) ⁶	F	0.7 (215)	-

Table 2. Breeding density and nest spacing of Black Kite populations in Europe and India (Delhi), 1966-2013.

Notes: Density was expressed as territorial pairs/10 km² for clarity of presentation. The 2013 data from the current study are presented twice in the table: (i) for the whole study area, i.e. representative of the whole Delhi population; and (b) for the high-density sector of the New Delhi National Zoological Park (NZP), in order to make them comparable to historical data from the 1970s by Malhotra (2007). Habitats are U. Urban: M. Marshland: FL. Farmland and Lake: WL. Woodland and Lake; F, Farmland; WP, Woodland and Pasture; WF, Woodland and Farmland; FL, Farmland and Lake; PW, Pasture and Woodland: RP. River Plain.

^aEstimate from Bustamante & Hiraldo (1990), for the period 1985-1988.

^bA single colony.

^cCalculated from the published map.

¹Thiollay (1967), ²Heckenroth (1970), ³Galushin (1971), ⁴Nore (1979), ⁵Sermet (1980), ⁶Fiuczynski (1981), ⁷Petretti & Petretti (1981), ⁸Hiraldo et al. (1990), ⁹De Giacomo et al. (1993), ¹⁰Viñuela et al.

(1994), ¹¹Henrioux & Henrioux (1995), ¹²Seelig et al. (1996), ¹³Sergio & Boto (1999), ¹⁴Sergio et al. (2003), ¹⁵Sergio et al. (2005), ¹⁶Malhotra (2007), ¹⁷This study.

fear of humans by most kites in comparison to European conspecifics. (3) Third, the city provides an environment with a low abundance of potential predators. The only potential nest predators known to occur locally are Indian Eagle Owls Bubo bubo bengalensis, House Crows Corvus splendens and Rhesus Macaques Macaca mulatta. The latter two species can be locally abundant, but are often deterred by the very aggressive and effective nest defence behaviour of parent kites.

When compared to historical records, the high density we recorded seemed remarkably stable over several decades. Rapid city-wide surveys and data from the New Delhi Zoological Park suggested only slightly higher densities in the 1970s than currently observed (Galushin 1971, Desai & Malhotra 1979; see Table 2). This is despite enormous changes in the city's dimensions, population size and management, and despite the recent, virtual extinction of the locally abundant populations of a potential trophic the White-rumped Vulture competitor, Gyps bengalensis, the former primary scavenger (Prakash et al. 2003, Naoroji 2006). The kite population thus seems very resilient to change in terms of overall density.

The laying season was protracted over almost four months, probably as a result of the long period of warm, favourable climate and of the stable food supply provided by the urban environment (Fig. 1). The temporal peak and range of laying dates seemed to be arranged so that most nestlings fledged well before the high temperatures and the marked peak in precipitation caused by Monsoon rains in July-August (Fig. 2). The negative effect of high temperatures and rainfall on kite foraging performance, egg viability and breeding success has been reported for various European populations (Hiraldo et al. 1990, Viñuela 2000, Sergio 2003). The observed, lengthy range of laying dates compares to a duration of the laying season of 28 days for kite populations of the Italian Alps and to 2.8 months for the population of Doñana National Park, in the extreme south of Europe (F. Sergio, pers. data). This suggests a North-South latitudinal gradient in the length of kites' breeding seasons. Protracted breeding seasons are increasingly reported as progressively more studies of birds of prey are conducted in tropical or more southern latitudes (Simmons 2000, Ogada & Kibuthu 2012).

When compared to other populations (review in Table 3), our estimates of breeding success were lower than in other studies and this may be a consequence of density-dependent processes in a crowded, saturated population (Newton 1998). The fact that similarly low levels of reproduction were reported for another saturated population (Doñana, Sergio et al. 2011) lends support to this impression. However, in the absence of more information, other alternative explanations

Mean number of fledged young

Table 3. Productivity of Black Kite populations in Europe and Asia, 1966–2013.

Area (period)	Habitat (n)	Clutch size	Hatching success ^a (eggs)	Breeding success (%)	lerritorial pair	Breeding pair	Successful pair
Delhi, India (2013) ¹¹	U (151)	2.09 (100) ^b	68% (157) ^b	48	0.73	1.09 (100) ^b	1.52 (72) ^b
NZP, India (1973–1976) ²	U (45)	2.3 (60) ^b	55% (102) ^b	-	0.98	_	_
NZP, India (2013) ¹¹	U(46)	2.04 (36)	62% (55) ^b	59	0.78	0.95 (38) ^b	1.44 (25) ^b
RBD, Spain (1989–2000) ¹⁰	WL(1059)	2.02	67.4 (416)	41	0.59	0.71	1.43
Matas Gordas, Spain (1992–2000) ¹⁰	GM(515)	2.12	70.3 (232)	44	0.61	0.85	1.46
Germany (1992–1995) ^{7c}	- (599)	_	_	79	1.63	_	2.07 (471) ^b
Limousin, France (1976–1978) ³	PW (22)	_	_	68	_	1.32	1.93 (15) ^b
Berlin, Germany (1940–1979) ⁴	F (215)	_	_	62	1.20		1.90 (133) ^b
Lake Lugano, Italy (1992–1996) ⁹	WL (143)	2.29 (42) ^b	84% (96) ^b	55	0.97	1.1 (95) ^b	1.78 (78) ^b
Lake Lugano, Italy (1992–2003) ¹⁰	WL (315)	2.3	74 (88)	50	0.90	1.24	1.80
Lake Maggiore, Italy (1996–2000) ¹⁰	WL (30)	_	_	50	0.87	_	1.73
Lake Como, Italy (1996–2000) ¹⁰	WL (40)	_	_	48	0.75	_	1.58
Lake Iseo, Italy (1996–2000) ¹⁰	WL (48)	_	_	38	0.48	_	1.10
Lake Idro, Italy (1997–2001) ¹⁰	WL (37)	_	_	59	1.05	_	1.63
Lake Garda, Italy (1997–2000) ¹⁰	WL (18)	_	_	44	0.83	_	2.14
Sarca Valley, Italy (1997–2003) ¹⁰	WL (88)	-	_	40	0.63	-	1.62
Slovakia (1975–1989) ⁵	- (162)	2.98 (44) ^b	_	-	-	2.31	-
Lac Leman, Switzerland (1975–1990) ⁸	FL (165)	2.25	_	_	-	2.02	_
Lorraine, France (1966) ¹	WP (66)	2.26 (45) ^b	_	_	1.32	1.58 (55) ^b	-
Nagasaki, Japan (1983–1986) ⁶	FP (32)	2.18 (28) ^b	79% (61) ^b	75	1.00	1.14 (28) ^b	1.33 (24) ^b

Notes: The 2013 data from the current study are presented twice in the table: (i) for the whole study area, i.e. representative of the whole Delhi population; and (ii) for the high-density sector of the New Delhi National Zoological Park (NZP), in order to make them comparable to historical data from the 1970s by Desai & Malhotra (1979). Habitats are U, Urban; GM, Grassland and Marshland; FL, Farmland and Lake; WL, Woodland and Lake; F, Farmland; WP, Woodland and Pasture; FL, Farmland and Lake; PW, Pasture and Woodland; FP, Fishing Port. ^aData on hatching success not shown in the table: 75% (*n* = 36 eggs from 14 nests, Hakel, Germany, 1957; Stubbe 1961) and 64% (*n* = 28 eggs from 10 nests, Lazio, Italy, date unknown; Petretti 1992).

^bSample size (when different from that in column 'Habitat (n)').

^cData also from Mammen & Stubbe (1995, 1996).

¹Thiollay (1967), ²Desai & Malhotra (1979), ³Nore (1979), ⁴Fiuczynski (1981), ⁵Danko (1989), ⁶Koga et al. (1989), ⁷Gedeon (1994)^c, ⁸Henrioux & Henrioux (1995), ⁹Sergio & Boto (1999), ¹⁰Sergio et al. (2005), ¹¹This study.

cannot be discounted: for example, it is not known whether a diet based in large portion on rubbish and meat produced for human consumption could spread pathogens or toxic substances among the offspring.

Finally, the observed diet composition confirmed the full dependence of the local kite population on urban resources, such as meat scraps from slaughterhouses or prey species which were extremely abundant within the city, such as rats, pigeons and doves. The current picture of the diet does not suggest that kites range frequently, if at all, out of the city to capture wild prey in surrounding rural areas. This confirms that the high density attained within the urban setting is likely promoted by attraction to a dense food source.

In summary, extensive foraging opportunities, a stable favourable climate, absence of human persecution and low density of potential predators have probably contributed to one of the densest raptor populations of the world. The current conservation status of the studied population seems satisfactory, but recent urban development is causing extreme and almost complete removal of mature trees in some sectors of the city. In turn, this could limit the kite population in the future, or trigger local declines and re-distributions, especially when considering that artificial structures do not seem to fully compensate for tree absence (authors' pers. data). Thus, given the abundance of the species and the current urban sanitary levels, the ecological service provided by kites through removal of organic rubbish must be valuable, suggesting the need for ecologically sensitive urban planning of the remaining green areas. This calls for the importance of continued monitoring of the population and its nesting requirements in future years.

ACKNOWLEDGEMENTS

We thank W. Cresswell and three anonymous reviewers for improving the manuscript with their comments. We thank the Forest Departments of the Government of NCT, Delhi and Uttar Pradesh; Shri. Amitabh Agnihotri (Director of the National Zoological Park, New Delhi); the Administrative Officer of Miranada House: University of Delhi (DU); various other landowners, managers and government officials for permissions and logistic support. We heartedly thank for help in the field our field assistant Vishnu Narayan, Dr A. Tanferna and the following volunteers of the 'Black Kite Project Group' from Sri Venkateswara College (DU) and the University of Delhi: M. Singh, N. Goyal, S. Gupta, E. Bhartia, A. Yadav, C. Prajapati, D. Pal, V. Sindhi, K. Wadhwa, D. Ramanan, S. Prajapati, N. Verma, J. Sungra, B. Roy, A. Bedi, A. Mandal, V. Gupta, A. Dutta, P. Kumar, Raju, D. Thakur, G. Singh, Saubhagya, G. Vashishtha and M. Garg.

FUNDING

The study was funded by the Wildlife Institute of India and Raptor Research and Conservation Foundation (RRCF, Mumbai). Funding for travelling and fieldwork by F. Sergio was afforded by Project RNM-7307 of the Junta de Adalucia and CGL2011-28103 of the Spanish Ministry of Science and Innovation.

REFERENCES

- Abdulali, H. 1968. Extension of the range of the large Indian Kite Milvus migrans lineatus (Gray). J. Bombay Nat. History Soc. 65: 774.
- Abdulali, H. 1972. Some bird notes by W.F. Sinclair. J. Bombay Nat. History Soc. 69: 422–424.
- Ali, S. 1926. Mating habits of the Common Kite Milvus migrans govinda. J. Bombay Nat. History Soc. 31: 524–526.
- Ali, S. & Ripley, S. D. 1983. Handbook of the Birds of India and Pakistan: together with those of Bangladesh, Nepal, Sikkim and Sri Lanka (Vol. 1: Divers and Hawks). Compact ed. Delhi (IN): Oxford University Press. p. 226–229.
- Bijlsma, R.G. 1997. Black Kite. In Hagemeijer, W.J.M. & Blair, M.J. (eds.) The EBCC Atlas of European Breeding Birds, their Distribution and Abundance, 132–133. T & AD Poyser, London.
- Blanco, G. 1997. Role of refuse as food for migrant, floater and breeding Black Kites (Milvus migrans). J. Raptor Res. 31: 71–76.
- Brown, L.H., Urban, E.K. & Newman, K. 1982. The Birds of Africa, Vol. 1. Academic Press, London.
- Bustamante, J. & Hiraldo, F. 1990. Adoptions of fledglings by Black and Red Kites. Anim. Behav. 39: 804–806.
- Census Organization of India. 2011. Census of India. Available from: http://censusindia.gov.in/2011census [accessed 27 September 2013].
- Champion, H.G. & Seth, S.K. 1968. A Revised Survey of the Forest Types of India. Manager of Publications, Government of India, New Delhi.
- Cramp, S. & Simmons, K.E.L. 1980. Handbook of the Birds of Europe, the Middle East and North Africa, Vol. 2. Hawks and Bustards. Oxford University Press, Oxford.
- Danko, Š. 1989. Five young in the nest of a Black Kite (Milvus migrans). Buteo 4: 87–92.
- De Giacomo, U., Martucci, O. & Tinelli, A. 1993. L'alimentazione del Nibbio bruno (*Milvus migrans*) nella Tenuta di Castelporziano (Roma). Avocetta. 17: 73–78.
- Desai, J.H. & Malhotra, A.K. 1977. Growth and development of the Pariah Kite Milvus migrans govinda. Miscellaneous Rep. Yamashina Inst. Ornithol. 9: 217–226.
- Desai, J.H. & Malhotra, A.K. 1979. Breeding biology of the Pariah Kite Milvus migrans at Delhi Zoological Park. Ibis 121: 320–325.
- Ferguson-Lees, J. & Christie, D.A. 2001. Raptors of the World. Houghton Miffin Company, New York.
- Fischer, C.E.C. 1906. Flocking of Kites. J. Bombay Nat. History Soc. 17: 525–526.
- Fiuczynski, V. 1981. Berliner milan-chronik (Milvus migrans and Milvus milvus). Beitr. Vogelkd 27: 161–196.
- Galushin, V.M. 1971. A huge urban population of birds of prey in Delhi India. *Ibis* **113:** 522.
- Gedeon, K. 1994. Monitoring Greifvögel und Eulen. Grundlagen und Möglichkeiten einer Langfristigen Überwachung von Bestandsgröben

und Reproduktionsdaten Jahresber. Monitoring Greifvögel Eulen Europas 1: 1–118.

- Hanxwell, T.A. 1892. Nest and eggs of the crested Black Kite. J. Bombay Nat. History Soc. 07: 403–404.
- Heckenroth, V. 1970. Der Greifvögelbestand des Bodanrücks (Bodensee) 1968 and 1969. Anz. Ornithol. Ges Bayern 9: 47–51.
- Henrioux, P. & Henrioux, J. 1995. Seize ans d'etude sur les rapaces diurnes et nocturnes dans l'Ouest lemanique (1975–1990). Nos Oiseaux 43: 1–26.
- Hiraldo, F., Veiga, J.P. & Manez, M. 1990. Growth of nestling Black Kites Milvus migrans: effects of hatching order, weather and season. J. Zool. Lond. 222: 197–214.
- India Meteorological Department. 2013. http://amssdelhi.gov.in/ climatology/sfd1.htm [accessed 27 September 2013].
- Koga, K., Siraishi, S. & Uchida, T.A. 1989. Breeding ecology of the Black-eared Kite Milvus migrans lineatus in the Nagasaki Peninsula, Kyushu. Jpn. J. Ornithol. 57: 57–66.
- Mahabal, A. & Bastawade, D.B. 1985. Population ecology and communal roosting behaviour of Pariah Kite Milvus migrans govinda in Pune (Maharashtra). J. Bombay Nat. History Soc. 82: 337–346.
- Malhotra, A.K. 1991. Site fidelity and power of recognition in Pariah Kite Milvus migrans govinda. J. Bombay Nat. History Soc. 87: 458.
- Malhotra, A.K. 2007. Tiger of sky-Pariah Kite. PhD Thesis, Shilalekh Publishers, Delhi.
- Mammen, U. & Stubbe, V. 1995. Jahresbericht 1994 zum monitoring Greifvögeln und Eulen Europas Jahresber. Monitoring Greifvögel Eulen Europas 7: 1–78.
- Mammen, U. & Stubbe, V. 1996. Jahresbericht 1995 zum monitoring Greifvögeln und Eulen Europas Jahresber. Monitoring Greifvögel Eulen Europas 8: 1–92.
- Naoroji, R. 2006. Birds of Prey of the Indian Subcontinent. Christopher Helm/A&C Black Publishers Ltd., London.
- Newton, I. 1998. Population Limitation in Birds. Academic Press, London.
- Nore, T. 1979. Rapaces diurnes communs en Limousin pendant la periode de nidification (Buse, Bondre, Milan noir, Busards saintmartin et Cendre). Alauda 47: 183–194.
- Ogada, D.L. & Kibuthu, P.M. 2012. Breeding ecology of Mackinder's Eagle-Owls (Bubo capensis mackinderi) in farmlands of central Kenya. J. Raptor Res. 46: 327–335.
- **Ortlieb, R.** 1998. Der Schwarzmilan. Die Neue Brehm-Bücherei, Hohenwarsleben, Germany.
- Owino, A., Biwott, N. & Amutete, G. 2004. Bird strike incidents involving Kenya Airways flights at three Kenyan airports, 1991– 2001. African J. Ecol. 42: 122–128.
- Petretti, F. 1992. Nibbio bruno. In Brichetti, P. De Franceschi, P. & Baccetti, N. (eds.) Fauna d'Italia, 459–465. Edizioni Calderini, Bologna, Italy.
- Petretti, A. & Petretti, F. 1981. A population of diurnal raptors in central Italy. Gerfaut 71: 143–156.
- Prakash, V., Pain, D.J., Cunningham, A.A., Donald, P.F., Prakash, N., Verma, A., Gargia, R., Sivakumar, S. & Rahmani, A.R. 2003. Catastrophic collapse of Indian White Backed (*Gyps bengalensis*) and Long Billed (*Gyps indicus*) vulture population. *Biol. Conserv.* **109**: 381–390.

- Satheesan, S.M. 1996. Raptors associated with airports and aircraft. In D. M. Bird, D. E. Varland, and J. J. Negro (eds.) Raptors in human landscapes: adaptations to built and cultivated environments: Adaptations to built and cultivated environments, 315–323. Academic Press, London.
- Seelig, K., Benecke, H., Braumann, F. & Nicolm, B. 1996. Die Vogel im Naturpark Drömling. Abh. Ber. Mus. Heineanum 3, Sonderh, Germany.
- Sergio, F. 2003. From individual behaviour to population pattern: weather-dependent foraging and breeding performance in Black Kites. Animal Behav. 66: 1109–1117.
- Sergio, F. & Boto, A. 1999. Nest dispersion, diet and breeding success of Black Kites (*Milvus migrans*) in Italian Pre-Alps. J. Raptor Res. 33: 207–217.
- Sergio, F., Pedrini, P. & Marchesi, L. 2003. Reconciling the dichotomy between single species and ecosystem conservation: Black Kites and eutrophication in pre-Alpine lakes. *Biol. Conserv.* 110: 101–111.
- Sergio, F., Blas, J., Forero, M., Fernández, N., Donázar, J.A. & Hiraldo, F. 2005. Preservation of wide-ranging top predators by site-protection: Black and Red kites in Doñana national park. *Biol. Conserv.* **125**: 11–21.
- Sergio, F., Blas, J., López, L., Tanferna, A., Díaz-Delgado, R., Donázar, J.A. & Hiraldo, F. 2011. Coping with uncertainty: breeding adjustments to an unpredictable environment in an opportunistic raptor. Oecologia 166: 79–90.
- Sermet, E. 1980. Milan noir. In Schifferli, A., Göroudet, P. & Winkler, R. (eds.) Arias des oiseaux nicheurs de Suisse, 88–89. Station Ornithologique de Sem-pach, Sempach, Switzerland.
- Simmons, R.E. 2000. Harriers of the World: Their Behaviour and Ecology. Oxford University Press, London, United Kingdom.
- Steenhof, K. 1987. Assessing raptor reproductive success and productivity. In B.A. Giron, P., Millsap B. A., Kline, K.W. & Bird D.M. (eds.) Raptor Management Techniques Manual, 157–170. Natl. Wildl. Fed., Washington, DC.
- Stubbe, V. 1961. Die Besiedelungsdichte eines Abgeschlossenen Waldgebietes (Hakel) mit Greifvögeln im Jahre 1957. Beitr. Vogelkd 7: 155–224.
- Thiollay, J.-M. 1967. Ecologie d'une population de rapaces diurnes en Lorraine. La Terre et la Vie. 114: 116–183.
- Thiollay, J.-M. & Bretagnolle, V. 2004. Rapaches nicheurs de France: distribution, effectifs et conservation. Delachaux et Niestlé, Paris, France.
- Viñuela, J. 1997. Laying order affects incubation duration in the Black Kite (*Milvus migrans*): counteracting hatching asynchrony? Auk 114: 192–199.
- Viñuela, J. 2000. Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. Behav. Ecol. Sociobiol. 45: 333–343.
- Viñuela, J., Villafuerte, R. & De Le Court, C. 1994. Nesting dispersion of a Black Kite population in relation to location of rabbit warrens. *Can. J. Zool.* 72: 1680–1683.
- Zar, J.H. 1984. Bio-Statistical Analysis, 283. Prentice-Hall, Englewood Cliffs, NJ.

(MS received 18 October 2013; revised MS accepted 15 December 2013)



Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools

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Abstract

Research in urban ecology is growing rapidly in response to the exponential growth of the urban environment. However, few studies have focused on tropical megacities, and on the interplay between predators' habitat selection and human socio-economic aspects, which may mediate their resilience and coexistence with humans. We examined mechanisms of breeding habitat selection by a synanthropic raptor, the Black Kite Milvus migrans, in Delhi (India) where kites mainly subsist on: (1) human refuse and its associated prey-fauna, and (2) ritualised feeding of kites, particularly practised by Muslims. We used mixed effects models to test the effect of urban habitat configuration and human practices on habitat selection, site occupancy and breeding success. Kite habitat decisions, territory occupancy and breeding success were tightly enmeshed with human activities: kites preferred areas with high human density, poor waste management and a road configuration that facilitated better access to resources provided by humans, in particular to Muslim colonies that provided ritual subsidies. Furthermore, kites bred at 'clean' sites with less human refuse only when close to Muslim colonies, suggesting that the proximity to ritual-feeding sites modulated the suitability of other habitats. Rather than a nuisance to avoid, as previously portrayed, humans were a keenly-targeted foraging resource, which tied a predator's distribution to human activities, politics, history, socio-economics and urban planning at multiple spatio-temporal scales. Many synurbic species may exploit humans in more subtle and direct ways than was previously assumed, but uncovering them will require greater integration of human socio-cultural estimates in urban ecological research.

Keywords Urban ecology · Food subsidies · Muslim · Ritual feeding · Synurbic · Urbanization

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11252-017-0716-8) contains supplementary material, which is available to authorized users.

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Introduction

Urban ecosystems are spreading rapidly, with more than 50% of the global human population currently concentrated in cities, a figure estimated to reach 66% by 2050 (United Nations 2014). Ninety-eight percent of this net increase is expected to happen in cities in developing countries (Grimm et al. 2008), so that by the middle of the twenty-first century 75% of urban dwellers will be located in Asia and Africa (Anonymous 2016). Such urban sprawl has well-demonstrated ecological consequences, including disruption of energy flow and nutrient cycles, habitat degradation, increased carbon emissions, and the extinction of many species (e.g. Pickett et al. 2001; McKinney 2010). Nevertheless, some animal species have managed to adapt and thrive under such conditions (Lepczyk et al. 2017), some for example can take advantage of human waste and reach densities that are not otherwise encountered (Brook et al. 2003; Gangoso et al. 2013; Inger et al. 2016). These urban exploiters are often alien invaders seen as 'nuisances to eradicate' (e.g. Belant 1997; Brook et al. 2003; Kurosawa et al. 2003), but can also be native species that have co-existed with humans for millennia, and so are pre-adapted to urban conditions and appreciated for their cultural significance (reviews in Hosey and Melfi 2014; Soulsbury and White 2015). Studying these synanthropic species is important for several reasons. First, they offer unique insight into the capacity of animals to withstand and even exploit human activity, thus adapting to a growingly urban world. Second, their abundance and frequent commensalism with humans makes them an integral part of the human cultural landscape, potentially making them important components of people's sense of connection with nature (e.g. Nilon 2011; Fuller et al. 2012; Cox and Gaston 2016). Third, many of them are facultative scavengers that subsist on animal carrion and human waste, thus providing fundamental ecosystem and sanitary services, as well demonstrated in urban and rural environments (e.g. Margalida and Colomer 2012; Gangoso et al. 2013; Moleón et al. 2014; Inger et al. 2016). Fourth, they are often dominant components of the community, potentially limiting other species, and thus contributing to faunal homogenization (McKinney 2006; Shochat et al. 2010; Carey et al. 2012). Finally, these species could indicate the future behavioural and demographic characteristics of exotic urban invaders when they reach a mature stage of colonization. However, despite all the above, relatively few intensive studies have centred on these 'synanthropic' urban exploiters (e.g. Marzluff et al. 2001; Parker and Nilon 2012).

While research on urban ecology grows exponentially (e.g. Mayer 2010), several areas have received limited attention. In particular, there is a paucity of intensive studies conducted in tropical regions (a severe deficiency highlighted by many reviews, e.g. Chace and Walsh 2006; Magle et al. 2012; Marzluff 2016), despite the fact that urbanization will be

heavily concentrated in such areas over the coming decades (Malakoff et al. 2016). Scarce research attention has also been devoted to megacities (cities with >10 million inhabitants), most of which are themselves concentrated in developing tropical countries (Grimm et al. 2008; Malakoff et al. 2016). Furthermore, few studies have focused on facultative scavengers or top predatory species, probably because much of the urban fauna is dominated by small species with diets dominated by plant material (e.g. Evans et al. 2011). Finally, despite the obvious significance of humans to the very existence of the urban environment, remarkably few authors have either incorporated human socio-economic factors as an integral component of their ecological research (e.g. Grimm et al. 2000; Liu et al. 2007), or focused on habitat selection by individual animals, which may yield important insight into mechanisms of resilience enabling close coexistence with humans.

To contribute to these overlooked areas, we examined habitat selection by a synanthropic native top predator in the tropical megacity of Delhi, India, currently the second most populous city in the world. Here we demonstrate that its habitat choices are tightly intertwined with human activities, including specific socio-religious practices, which greatly influence the spatial distribution of food subsidies.

Methods

Model species

The Black Kite Milvus migrans (hereafter kite) is a mediumsized opportunistic raptor, widely distributed throughout Eurasia, Africa and Australia, and considered as the most successful raptor in the world. In India, the native, resident subspecies M. m. govinda is synurbic (Francis and Chadwick 2012), i.e. occurring almost exclusively in close association with humans in towns and cities (Naoroji 2006). In Delhi, kites breed on both trees and artificial structures (pylons, towers), sometimes forming loose colonies and locally reaching extremely high densities, thanks to the exploitation of human food subsidies facilitated by inefficient refuse disposal and by religious kite-feeding practices (Kumar et al. 2014; see details below). These large-scale subsidies may explain Delhi's capacity to host what is probably the largest raptor concentration in the world (Galushin 1971; Kumar et al. 2014).

Study area

Delhi is a megacity of more than 16 million inhabitants, currently covering an area of 1500 km^2 and in constant, rapid expansion (Census organization of India 2011). It is polycentric and heterogeneous, with a multitude of urban configurations, which make it difficult to establish a linear urban-rural gradient. The climate is semi-arid, with a mean annual precipitation of 640 mm, mainly concentrated in July and August during the monsoon season. Temperature ranges from a minimum mean value of 8.2 °C in the winter to a maximum mean value of 39.6 °C during the summer (Indian Metrological Department 2013). The vegetation of the general region falls within the 'northern tropical thorn forest' category (Champion and Seth 1968).

Two aspects of Delhi are important for kite foraging. First, large portions of the city are characterized by poor solid waste management, which affords plenty of food to kites in the form of carrion or refuse, and its associated prey-fauna (e.g. rodents, pigeons etc.). Second, many people engage in the centuries-old religious practice of feeding meat scraps to kites (hereafter termed "ritualized-feeding") typically offered by throwing meat into the air for the birds to catch. These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries (Pinault 2008; Taneja 2015). Whilst meat-offering is practiced by a number of communities, in Delhi it is especially prevalent amongst members of the Muslim faith, whose numbers are concentrated in well-defined portions of the city (hereafter "Muslim colonies"). In these areas, ritualized-feeding is operated both by private individuals, and as public events, typically around mosques, where large quantities of meat are tossed to kites at predictable hours each day, sometimes causing hundreds of kites to congregate. Thus, waste management issues common to all communities, and cultural rituals which are more specific to some, generate spatial heterogeneity in the potential food availability for kites.

Field procedures

We surveyed kite nests systematically over the four years 2013-2016 at 24 plots of 1 km². These were plotted randomly within Delhi (1500 km²) so as to cover all its possible urban settings, from semi-natural to extremely built-up sites (details in Kumar et al. 2014). This resulted in a sample of 154 nests, each from a different territory, used at least once for breeding between 2013 and 2016. Nests were checked every 7–10 days until the chicks were at least 45 days old, in order to estimate the number of young raised to fledging (chicks fledge when about 48 days old; see Kumar et al. 2014 for further details of nest checks and surveys).

Breeding site characteristics

To investigate nest-site selection, we compared the urban, human and environmental variables collected at the 154 nests (see below) with those collected at an equal number of random locations, generated through ArcGIS 10.0 as follows. For each sample plot, we drew a circle of 5 km-radius centred on its barvcentre (arithmetic centre of its outline-corners, as calculated by ArcGIS 10.0) and plotted within it a number of random locations equal to the number of real nests censused in that plot (i.e. if a plot contained X nests, we plotted X random locations within its 5 km radial area). The radius of 5 km was chosen because floating, pre-breeding kites frequently prospect 7-10 km wide areas when choosing where to settle to breed (Tanferna et al. 2013; authors' unpubl. GPS-data). Thus, we assumed that each individual could compare the habitat configuration of the location eventually chosen with potential, alternative sites within a 5 km radius, an area that would be easy to observe in its entirety by a high circling kite on a clear day. Once plotted by GIS, we: (1) visited each random location using a handheld GPS; and (2) repositioned the location on the nearest tree or artificial structure judged capable of supporting a kite nest (e.g. with a sufficiently high, solid fork, based on our previous experience in observing hundreds of kite nests).

The variables recorded at each nest or random location are detailed in Online Resource 1 Table A1, they were devised on the basis of our knowledge of local kite ecology, and measured vegetational, urban and human features at three "scales". The "nest area" scale estimated the characteristics of the potential nesting tree or artificial structure and its immediate surroundings, such as the height of the nesting structure, woodlot size, or whether the nesting tree was isolated or in a hedgerow, parkland or woodlot (Online Resource 1, Table A1). The "landscape scale" (hereafter "urban scale") measured the urban configuration and landscape structure within 500 m of each sample location, such as indices of road and building density, or percentage and diversity of land-cover types (Online Resource 1, Table A1). It also included the proximity to potentially important features, such as roads, water or rubbish dumps. The 500 m radius was arbitrarily chosen because this is the area around the nest most intensively patrolled for hunting by breeding individuals, especially females, based on intensive observation of focal pairs. Finally, the "human scale" provided direct and indirect estimates of human activities and practices, such as distance to Muslim colonies, efficiency of waste management, or human density. Several of these variables directly or indirectly estimated the potential access of kites to different types of human subsidies, as detailed in Online Resource 2. Nest-area characteristics were measured in the field with a metric tape. Measures of proximity and surface cover, such as distance to roads or woodlot size were assessed in Google Earth Pro and ArcGIS 10.0. Human variables, such as hygiene score or human density, were recorded through ground surveys and interviews with local people (see Online Resource 2 for details).

Statistical analyses

We used t-tests and χ^2 tests to explore differences between kite nests and random locations. We then employed a mixed model logistic regression (Zuur et al. 2009) with a backward stepwise procedure to examine the nest-area, urban and human factors (Online Resource 1, Table A1) discriminating between kite nests and random locations. Of the total 308 available locations, we randomly selected 100 nests and 100 random sites for model building, and employed the remaining 54 nests and 54 random locations for model validation (Fielding and Haworth 1995). Because multiple nests and random locations were drawn from the same plot and its surroundings, and thus were closer to each other than those from other, more distant, sample plots, plot ID was added as a random factor.

To reduce collinearity and the number of variables presented to the logistic regression, we employed the method of variable reduction proposed by Green (1979) and commonly employed in habitat selection studies (e.g. Austin et al. 1996; Soh et al. 2002). In this method, pairs of strongly inter-correlated variables (r > 0.60) are considered as estimates of a single underlying factor, and only one of the two is retained for analysis, usually the one likely to be perceived as more important by the study organism. Collinearity was subsequently checked further by examining the variance inflation factors (VIF) of the explanatory variables, which were always low (< 2; Crawley 2007; Zuur et al. 2009).

Some of the kites of our study population were GPS-tagged as part of a parallel study on their movement ecology. Because these individuals visited multiple Muslim colonies, and because large numbers of kites (e.g. > 100) were seen to assemble during ritual-feeding episodes, suggesting congregation from distant sites, we decided to estimate the distance of each nest or random location from multiple Muslim colonies. When we compared such distances between nests and random points in exploratory analyses, kites seemed to over-select sites closer than available to the 1st, 2nd and, possibly, 3rd closest colony, after which the difference became unimportant (Online Resource 3). Thus, to provide a comprehensive measure that integrated the proximity to the three nearest Muslim colonies with their human population density (under the assumption that higher rates of refuse and ritualized-feeding should occur in denser colonies), we extracted the first component of a PCA (Tabachnick and Fidell 1996) run on these four aforementioned variables. Its PC1 (hereafter "access to Muslim subsidies") explained 65% of the variance and had a high positive loading on Muslim population density and high negative loadings on the distance to the 1st, 2nd and 3rd closest Muslim colonies. Thus, it provided an increasing index of access to abundant "Muslim subsidies" and was fitted to all models (Online Resource 1, Table A3).

To gain a deeper understanding of habitat quality available to kites, and to test whether the observed habitat choices were adaptive (e.g. Clark and Schutler 1999; Sergio et al. 2003), we used linear mixed models. These again used plot ID as a random factor and tested the effect of the same set of variables presented

to the habitat selection logistic model on both the number of years that a territory was occupied and on the cumulative number of fledglings that it produced between 2013 and 2016. We predict that territories that were more frequently occupied were of higher quality and thus were more attractive to kites, as has been demonstrated in other avian species, including other kite populations (review in Sergio and Newton 2003).

All multivariate models were built by a frequentist approach through a backward stepwise procedure following Zuur et al. (2009): all explanatory variables were fitted to a maximal model, extracted one at a time from the maximal model, and the associated change in model deviance was assessed by the significance of a likelihood-ratio test; the procedure was repeated until we obtained a final model which only included significant variables (Zuur et al. 2009). To avoid over-parameterization, we ensured never to fit more than N/3variables to each maximal model, where N is the sample size of the analyzed dataset (Crawley 2007). Interactions were fitted only when we had a priori hypotheses about their potential effect, based on our field observations and knowledge of the population. In particular, we hypothesized that the selection of green cover, urban cover or hygiene level could be conditional upon proximity to Muslim subsidies, because the latter could affect habitat and food profitability. We also hypothesized that the preference for a low level of hygiene (i.e. for high human waste availability) could depend on human density and vice versa, and thus fitted the interaction between hygiene score and human density. Model assumptions were checked by investigating QQ plots, histograms of residuals, and plots of standardized and normalized residuals against fitted values and against explanatory variables (Crawley 2007; Zuur et al. 2009). All GLMMs were implemented in R.3.0.2 (R Development Core Team 2009). When necessary, variables were logarithmically, or arc-sine square root transformed in order to achieve a normal distribution. All tests are two-tailed, statistical significance was set at $\alpha < 0.05$, and all means are given ± 1 SE.

Results

In univariate tests (Online Resource 1, Table A2), at the nestarea scale, kites did not prefer trees over artificial structures, although most nests (87%) were built in trees. There was also no clear preference for tree species, with kites opportunistically using 13 different tree species (Online Resource 4). Instead, they seemed more selective of the arrangement of trees, overselecting woodlots and parklands rather than single trees or lines of trees (Fig. 1a). Also, when they nested in woodlots, they selected larger woodlots than the average available (Online Resource 1, Table A2). At the urban scale, kites preferred sites with lower human housing densities, lesser extents of built-up surfaces, higher availability of roads and woodland, Fig. 1 Tree arrangement (Panel a), and index of road density, percentage urban land cover within a 500 m radius, and human density (panel b) at 100 Black Kite nests (black bars) and 100 random locations (white bars) in Delhi (India)



and higher habitat diversity (Online Resource 1, Table A2). Finally, kite nests differed from random locations for all human variables. Compared to availability, nests had higher access to Muslim subsidies, higher density of Muslim inhabitants, higher human density in the streets and greater quantities of anthropogenic refuse (Online Resource 1, Table A2).

According to the logistic model discriminating between kite nests and random locations (Online Resource 1, Table A3a), kites preferentially selected sites in woodland, with higher road density, with less urban cover and greater woodland extent at the landscape scale, with higher human densities in the streets, lower hygiene levels and greater access to Muslim subsidies (Fig. 1a, b; 2b). The interaction of access to Muslim subsidies with hygiene score and with woodland land-cover also entered the model (Online Resource 1, Table A3a): first, low-refuse sites were selected if found close to Muslim colonies, while locations with much refuse were over-selected when far from Muslim subsidies (Fig. 3). Second, large woodland extents were preferred close to Muslim colonies but avoided when far from them (Fig. 2a, b). The logistic model performed well when reapplied on both the training and validation datasets: it correctly reclassified 87% of the 200 locations used for model building (87% of 100 nests and 87% of 100 random sites), and 82% of the 108 locations set apart for validation (97.4% of 54 nests and 74.1% of 54 random sites).

Finally, both territory occupancy and breeding output were higher for territories with higher access to Muslim subsidies, and for those located in parkland and woodland (Online Resource 1, Table A3b, c).

Discussion

Our study offers a clear example of cities as complex ecosystems that link society and biota at multiple spatio-temporal scales. In particular, integrating human activities and practices with ecological processes at vast spatial scales allowed us to investigate resources which would have otherwise been missed by conventional ecological analyses of urban landcover. This reinforces the call for improved integration of socio-economic approaches to urban ecology, which will often require a reconceptualization of humans and their activities (Pickett et al. 2001; Grimm et al. 2008; Esbjorn-Hargens and Zimmerman 2009; Warren and Lepczyk 2012). Furthermore, the high predictive power of our logistic model of nest-site selection highlighted the importance of habitat models as potential conservation tools for urban planning (for integration of modelling and conservation in urban settings, see examples and reviews in Gordon et al. 2009; Kowarik 2011; Lepczyk and Warren 2012; Lerman et al. 2014).

Overall, our model suggested that Delhi Black Kites selected several socio-ecological features at multiple scales, from local tree-arrangement, to neighbourhood-level landscape structure, to the larger-scale spatial zoning of access to subsidies provided by human socio-religious practices (see below). Thus, the city was not homogenous in its suitability for kites, as might be assumed from their apparently constant presence throughout the city (e.g. Galushin 1971), which is typical of many facultative scavengers and synurbic species capable of consuming human waste (e.g. Sorace 2002; Brook et al. 2003). On the contrary, kites avoided monotonously built-up portions of the city and over-selected sites according to the following, very specific urban templet.

First, our model suggested that, compared to availability, kites over-selected woodland patches and avoided isolated trees or lines of trees. Woodlots may allow a more favourable micro-climate in a hot tropical city (e.g. Wang et al. 2015). They may also provide higher nest-site availability and thus accommodate a loose kite colony, with consequent potential advantages in turn of conspecific cuing to locate food (e.g. Valone and Templeton 2002; Danchin et al. 2004), likely to be important in this species (Sergio 2003, Sergio and Penteriani 2005) and in this population in particular (see below). The fact that the rate of selection increased from single trees (strongly avoided), to lines of trees (moderately avoided), to parkland (used as available) and then woodland (Fig. 1a) conforms to a progression of attraction to structural arrangements facilitating increasing levels of conspecific proximity. A preference for large patches of parkland and woodland has previously been demonstrated for other raptors inhabiting urban areas (e.g. Hogg and Nilon 2015, McPherson et al. 2016; Morrison et al. 2016) and confirms the importance of the abundance and arrangement of green vegetation for urban biota (Lepczyk et al. 2017).

Second, while kites avoided high rates of built-up land cover, they simultaneously selected areas with high road and human density. Because human density was assessed in the streets, it equated to an index of human traffic and street-activity, and because refuse is often disposed of by people in a disorganized and unpredictable manner in Delhi, high levels of human activity in the streets likely implies more waste accumulation in these areas. This may provide food directly for kites or for co-occurring species that may in turn represent live prey for kites, such as small mammals or pigeons. Thus, kite's habitat decisions seemed to be set not simply on human density per se, which would probably be higher in densely built-up areas (actually avoided), but more specifically on a high density of roads with intense human activity. In this sense, urban configuration was important as it 'structurally' mediated the kites' access to the functionally relevant portion of the human population. In agreement with this interpretation, we have frequently observed hunting kites quartering over roads, or moving through a series of dominant perches, intently 'observing' human traffic in the streets below. Furthermore, the kites' preference for neighbourhoods with less efficient waste management further reinforced the idea that the link with human streetactivities was ultimately aimed at refuse exploitation. These analyses confirm the need to integrate conventional variables describing the urban landscape with more direct measures of human activities and practices, as highlighted by various authors (e.g. Alberti 2008, Pickett et al. 2001; Grimm et al. 2008; Warren and Lepczyk 2012).

Third, kites over-selected sites that allowed ready access to multiple Muslim colonies, i.e. to concentrations of people whose activities increased the availability of easy food. While several previous studies have investigated the effect of human subsidies on urban taxa, they have usually focused on garden-feeding operated by citizens of the northern hemisphere as a leisure activity (e.g. Fuller et al. 2012; Lepczyk et al. 2012; Cox and Gaston 2016). In our case, the spatial association of ritualized-feeding with certain religious communities completed the picture of these previous studies by adding a further socio-cultural component, which strongly characterizes the urban settings of large portions of southern Asia (see also Keniger et al. 2013). In our specific case, the ritual of tossing meat to kites, which is a widespread practice operated daily at predictable public sites, especially among members of the Muslim communities, has probably generated a mosaic of patches with high input of human subsidies. In agreement with this, our GPS-tagged kites regularly visited these sites with very deliberate-directed journeys to them and large numbers of kites, sometimes into the hundreds, were regularly seen to gather quickly during ritual-feeding episodes. However, this high level of congregation may also enhance competition, lowering the predictability of successful access to the subsidy at the individual kite level. This may explain the preference for proximity to multiple Muslim colonies, each one with multiple ritual-feeding sites, as this will allow each individual dozens of daily opportunities to access subsidies. Furthermore, strategic positioning of the nest within 1–2 km of multiple Muslim colonies may allow kites to spot flocks of conspecifics exploiting feeding-rituals, which are conspicuous even to humans, and to join them rapidly through conspecific cueing, as reported for kites in more natural environments (e.g. Sergio 2003). Note that the ability to exploit sudden flushes of easy food is one of the defining characteristics of this highly opportunistic species even in rural settings (Blanco 1997; Viñuela 2000), an ability which may have further pre-adapted it to life in a megacity. The above described coincidence of resource predictability, opportunism, high sociality, and high visibility of conspecific behaviour represents a typical scenario for the evolution of behavioural strategies based on conspecific cueing and attraction (e.g. Valone and

Fig. 2 Urban kites in Delhi selected sites for which access to Muslim colonies and vegetation cover positively covaried (panel a). Thus, they over-selected areas with abundant vegetation close to dense Muslim colonies, but avoided them when far from Muslim colonies (panel b). Access to Muslim colonies was estimated by means of a principal component analysis (see Methods) and portrayed as a categorical progression in panel b for clarity of presentation. Error bars represent 1 SE, black points/ bars portray kite nests and white points/bars represent random locations


Templeton 2002; Danchin et al. 2004). The advantages described above were confirmed by the higher occupation rate and breeding output of territories in proximity to multiple Muslim colonies, which suggested that these sites were attractive to kites, that they contributed a disproportionate number of fledglings to the population, and that the observed habitat choices were adaptive in terms of offspring production (i.e. over-selection of sites which offer a reproductive reward).

Fourth, the importance of strategic proximity to Muslim colonies was further confirmed by its interaction with other habitat features. Compared to a random distribution, kites over-selected sites for which green cover and access to Muslim colonies covaried positively (Fig. 2a). This implied that, close to Muslims, kites preferred neighbourhoods with abundant green cover, which may accommodate more nests and facilitate colony-formation, with potential benefits in terms of conspecific cueing (e.g. being alerted of the start of feeding-rituals by the departure of nearby conspecifics). Ultimately, this should allow density to be fine-tuned on food availability (larger densities close to large food concentrations). On the contrary, in scenarios of low food availability (low access to Muslim colonies, Fig. 2b), kites preferred sites with low green cover, which will limit density, thus lowering competition for limited food. Furthermore, the preference for proximity to Muslim colonies was especially pronounced in neighbourhoods where human refuse was scarce (Fig. 3). When hygiene levels were already low, food was likely available in the immediate nest surroundings, allowing kites to be less dependent on Muslim colonies and to nest farther from them. These results suggest that (a) access to hotspots of ritualizedfeeding modulated the suitability of other habitats, even when these were located kilometres away from such sites, which functionally integrated far-away components of the urban ecosystem (see also Grimm et al. 2000; Alberti 2008); (b) ritualized subsidies and waste production/disposal seemed to be the two pillars that directly or indirectly permeated all habitat preferences; and (c) kites seemed to strategically balance their access to these two factors in their habitat choices.

Overall, kite habitat decisions were tightly intertwined with human activities. They preferred sites with extensive access to roads busy with humans, with inefficient waste management and ready access to ritual cultural practices conducive to food subsidies. To date, humans have often been seen as obstacles. threats or nuisances that animal species have to deal with in order to 'tolerate' urbanization (e.g. Soh et al. 2002; Chace and Walsh 2006; McPherson et al. 2016). However, for many urban species, the attraction to an extreme anthropogenic ecosystem is based on the exploitation of human provision itself rather than resilience to its actions, and for some synanthropic species this may derive from millennia of co-existence with man, better seen as an integral portion of their niche as well as a beneficiary of ecosystem services (e.g. Marzluff and Angell 2005; Gangoso et al. 2013). In our system, Delhi kites cannot be thought of in isolation from humans and their voluntary and involuntary subsidies, which would qualify them as anthropophilic and anthropodependent species (sensu Hulme-Beaman et al. 2016). While the importance of human subsidies in altering the mosaic of foraging opportunities for animals is well appreciated (Fuller et al. 2012; Lepczyk et al. 2012; Oro et al. 2013; Newsome et al. 2014), in our case the subsidy-mosaic was uniquely tied to a complex array of human themes, such as (1) the Indian-level and local-level history of Muslim displacements, which followed India's independence and which determined the current distribution of Muslim colonies; (2) the global economy that drives urban sprawl, as well as the local economics of trade, which influenced the stability of some historical Muslim colonies; (3) the municipal planning of the currently skyrocketing urban expansion, which affects road and vegetation arrangement, as

Fig. 3 Access to dense Muslim colonies was higher at Black Kite nests (black bars) than at random locations (white bars) when local hygiene levels were high, while inefficient refuse disposal (i.e. low local hygiene) "released" kites from dependency on Muslim ritual subsidies. Error bars represent 1 SE



well as the efficiency of refuse disposal; and (4) the temporal dynamicity of cultural and religious practices, such as ritualized-feeding, which originated among Hindus but is currently prevalent among Muslim groups (e.g. Gupta 1998; Pinault 2008; Sharan 2014; Paul and Nagendra 2015; Taneja 2015). All the above tied kites' habitat choices to the spatial endresults of human activities shaped by history, socio-economics, politics, tradition and religion. Also, these links acted at time scales ranging from decades to centuries and at spatial scales ranging from neighbourhood to global. We believe that similarly tight and complex relations will apply to many other synurbic species worldwide (Francis and Chadwick 2012).

Conservation implications

The preference for certain amounts and configurations of woodland makes room for potential modulation of kite density through urban planning, as proposed for crows in Singapore (Soh et al. 2002). For example, promotion of woodlots close to areas with problematic refuse disposal may improve the potential ecological service provided by kite consumption of organic waste, a benefit that could be confirmed through adaptive management. Over the longer-term, waste disposal will be likely rationalized, mechanized and often processed indoor, as progressively legally enforced in developed countries. This will likely imply major declines in kite food availability, which could be partly buffered by planned maintenance and promotion of ritual feeding practices, seen as a unique connection between human culture and ecological function in rapidly expanding urban ecosystems (see below).

The close connection of urban kites to human activities, and their wide-ranging behaviour, typical of mobile avian predators, which tied them to far away sectors of the city, make them an ideal indicator species that integrates processes occurring at different scales of the urban landscape. In particular, the dependency of an urban top predator on ritual feeding, human culture and religion, which promotes one of the largest predator concentrations in the world (Kumar et al. 2014), could be seen as a socio-cultural and ecological uniqueness that connects urban dwellers with nature and has to be attentively preserved, just as an urban green space. In this context, investigation and documentation of the sociohistorical aspects and ecological implications of ritual feeding should be actively promoted.

As any megacity, Delhi is likely to change rapidly in coming decades in terms of sprawl, internal structure, management and culture (Grimm et al. 2008; Sharan 2014; Srivastava 2015). Modernization will sooner or later rationalize refuse disposal and younger generations already seem less interested in cultural practices such as ritualized-feeding (authors unpubl. Data), which will imply major shifts in resource availability and a threat to a unique system of human-predator coexistence.

Such conundrums between modernization, improving human conditions and protecting unique eco-cultural treasures such as the ritual feeding of kites will be formidable challenges to urban planning for innumerable, fast-growing towns and cities of the developing world (e.g. Gangoso et al. 2013).

Acknowledgements We thank Prof. Nilon and two anonymous reviewers for constructive comments on an earlier draft of the manuscript. We are grateful to Ben Sheldon, Chris Perrins, Tommaso Pizzari, Ujiwal Kumar, L. Agarwal and the Director. Dean and research coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Civic bodies of the Government of NCT of Delhi helped with legal permits, and Mr. A. Agnihotri, Director of the National Zoological Park of New Delhi provided accommodation and gave permission to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We express our most heartfelt gratitude to N. Shehzad and M. Saud of Wildlife Rescue for providing essential information, and to all the volunteers of the "Black Kite Project Group" from the University of Delhi (Sri Venkateswara and Deshbandhu Colleges), especially R. Prajapati, R. Negi, B. Sharma, P. Kumar and M. Singh who provided essential field help, enthusiasm and cooperation in the environmental education of locally assembling crowds of curious people. Special thanks to our field assistant Laxmi Narayan, who was the backbone of the field team. Finally, thanks to all the landowners, managers and government officials who patiently cooperated with our constant requests of access. The project was funded through grants by the Raptor Research and Conservation Foundation (Mumbai) and by the Govt. of India, Ministry of Environment, Forest and Climate Change. N Kumar's D. Phil at the University of Oxford was funded by the Felix Scholarship Trust. Funding for travelling and fieldwork by F. Sergio was afforded by Project RNM-7307 of the Junta de Andalucía and CGL2015- 69445-P of the Spanish Ministry of Economy and Competitiveness.

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References

- Alberti M (2008) Advances in urban ecology: integrating humans and ecological processes in urban ecosystems. Springer, New York. https://doi.org/10.1007/978-0-387-75510-6
- Anonymous (2016) Rise of the city. Science 352:906-907
- Austin GE, Thomas CJ, Houston DC, Thompson BA (1996) Predicting the spatial distribution of buzzards *Buteo buteo* nesting areas using a geographical information system and remote sensing. J Appl Ecol 33(6):1541–1550. https://doi.org/10.2307/2404792
- Belant JL (1997) Gulls in urban environments: landscape-level management to reduce conflict. Landsc Urban Plan 38(3-4):245–258. https://doi.org/10.1016/S0169-2046(97)00037-6
- Blanco G (1997) Role of refuse as food for migrant, floater and bredding black kites (*Milvus migrans*). Journal of Raptor Research 31:71–76
- Brook BW, Sodhi NS, Soh NCK, Chuam Lim H (2003) Abundance and projected control of invasive house crows in Singapore. J Wildl Manag 67(4):808–817. https://doi.org/10.2307/3802688
- Carey MP, Sanderson BL, Barnas KA, Olden JD (2012) Native invaders: challenges for science, management, policy, and society. Frontiers in. Ecol Environ 10(7):373–381. https://doi.org/10.1890/110060

- Census organization of India (2011) Census of India. http://censusindia. gov.in/2011census. Accessed 25 February 2017
- Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plan 74(1):46–49. https://doi.org/10.1016/j. landurbplan.2004.08.007
- Champion HG, Seth SK (1968) A revised survey of the Forest types of India. Manager of Publications, Government of India, New Delhi
- Clark RG, Schutler D (1999) Avian habitat selection: pattern from process in nest-site use by ducks? Ecology 80(1):272–287. https://doi.org/ 10.1890/0012-9658(1999)080[0272:AHSPFP]2.0.CO;2
- Cox DTC, Gaston KJ (2016) Urban bird feeding: connecting people with nature. PLoS One 11(7):e0158717. https://doi.org/10.1371/journal. pone.0158717
- Crawley MJ (2007) The R book. Wiley Press, Chichester. https://doi.org/ 10.1002/9780470515075
- Danchin É, Giraldeau L, Valone TJ, Wagner RH (2004) Public information: from noisy neighbors to cultural evolution. Science 305(5683): 487–491. https://doi.org/10.1126/science.1098254
- Esbjorn-Hargens S, Zimmerman ME (2009) Integral ecology: uniting multiple perspectives on the natural world. Integral Books, Boston
- Evans KL, Chamberlain DE, Hatchwell BJ, Gregory RD, Gaston KJ (2011) What makes an urban bird? Glob Chang Biol 17(1):32–44. https://doi.org/10.1111/j.1365-2486.2010.02247.x
- Fielding AH, Haworth PF (1995) Testing the generality of bird-habitat models. Conserv Biol 9(6):1466–1481. https://doi.org/10.1046/j. 1523-1739.1995.09061466.x
- Francis RA, Chadwick MA (2012) What makes a species synurbic? Appl Geogr 32(2):514–521. https://doi.org/10.1016/j.apgeog.2011.06. 013
- Fuller RA, Irvine KN, Davies ZG, Armsworth PR, Gaston KJ (2012) Interactions between people and birds in urban landscapes. Avian. Biology 45:249–266
- Galushin VM (1971) A huge urban population of birds of prey in Delhi India. Ibis 113:522
- Gangoso L, Agudo R, Anadón JD, dela Riva M, Suleyman AS, Porter R, Donázar JA (2013) Reinventing mutualism between human san wild fauna: insights from vultures as ecosystem services providers. Conserv Lett 6(3):172–179. https://doi.org/10.1111/j.1755-263X. 2012.00289.x
- Gordon A, Simondson D, White M, Moilanen A, Bekessy SA (2009). Integrating conservation planning and landuse planning in urban landscapes. Landsc Urban Plan 91(4):183–194. https://doi.org/10. 1016/j.landurbplan.2008.12.011
- Green RH (1979) Sampling design and statistical methods for environmental biologists. John Wiley and Sons, New York
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and ecology of cities. Science 319(5864):756–760. https://doi.org/10.1126/science.1150195
- Grimm NB, Steward JMG, Pickett TA, Redman CL (2000) Integrated approaches to long-term studies of urban ecosystems. Bioscience 50(7):571–584. https://doi.org/10.1641/0006-3568(2000) 050[0571:IATLTO]2.0.CO;2
- Gupta N (1998) Delhi between two empires, 1803–1931: society, government, and urban growth. Oxford University Press, New Delhi
- Hogg JR, Nilon CH (2015) Habitat associations of birds of prey in urban business parks. Urban Ecosyst 18(1):267–284. https://doi.org/10. 1007/s11252-014-0394-8
- Hosey G, Melfi V (2014) Human-animal interactions, relationships and bonds: a review and analysis of the literature. Int J Comp Psychol 27:117–142
- Hulme-Beaman A, Dobney K, Cucchi T, Searie JB (2016) An ecological and evolutionary framework for commensalism in anthropogenic environments. Trends Ecol and Evol 31(8):633–645. https://doi. org/10.1016/j.tree.2016.05.001
- Indian Metrological Department (2013) http://amssdelhi.gov.in/ climatology/sfd1.htm. Accessed 27 January 2017

- Inger R, Cox DTC, Per E, Norton BA, Gaston KJ (2016) Ecological role of vertebrate scavengers in urban ecosystems in the UK. Ecol Evol 19:7015–7023
- Keniger LE, Gaston KJ, Irvine KN, Fuller RA (2013) What are the benefits of interacting with nature? J Environ Res Public Health 10: 913–935
- Kowarik I (2011) Novel urban ecosystems, biodiversity, and conservation. Environ Pollut 159(8-9):1974–1983. https://doi.org/10.1016/j. envpol.2011.02.022
- Kumar N, Mohan D, Jhala YV, Qureshi Q, Sergio F (2014) Density, laying date, breeding success and diet of black kites *Milvus migrans* govinda in the city of Delhi (India). Bird Study 61(1):1–8. https:// doi.org/10.1080/00063657.2013.876972
- Kurosawa R, Kanai Y, Matsuda M (2003) Conflict between human and crows in greater Tokyo. Global. Environ Res 7:139–147
- Lepczyk CA, Aronson MFJ, Goddard MA, Lerman SB, Malvor JS (2017) Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. Bioscience 67(9):799–807. https://doi.org/10.1093/biosci/ bix079
- Lepczyk CA, Warren PS (2012) Urban bird ecology and conservation. University of California Press, Berkeley. https://doi.org/10.1525/ california/9780520273092.001.0001
- Lepczyk CA, Warren PS, Machabée L, Kinzig AP, Mertig AG (2012) Who feeds the birds? A comparison across regions. In: Lepczyk CA, Warren PS (eds) Urban bird ecology and conservation. University of California Press, Berkeley, pp 267–286. https://doi.org/10.1525/ california/9780520273092.003.0017
- Lerman SB, Nislow KH, Nowak DJ, DeStefano S, King DI, Jones-Farrand T (2014) Using urban forest assessment tools to model bird habitat potential. Landsc Urban Plan 122:29–40. https://doi.org/10. 1016/j.landurbplan.2013.10.006
- Liu J et al (2007) Complexity of coupled human and natural systems. Nature 31:1513–1516
- Magle SB, Hunt VM, Vernon M, Crooks KR (2012) Urban wildlife research: past, present, and future. Biol Conserv 155:23–32. https://doi.org/10.1016/j.biocon.2012.06.018
- Malakoff D, Wigginton NS, Fahrenkamp-Uppenbrink J, Wible B (2016) Rise of the urban planet. http://www.sciencemag.org/news/2016/05/ rise-urban-planet. Accessed 12.10.16
- Margalida A, Colomer MA (2012). Modelling the effects of sanitary policies on European vulture conservation. Sci Rep 2:753. https:// doi.org/10.1038/srep00753
- Marzluff JM (2016) A decadal review of urban ornithology and a prospectus for the future. Ibis 159:1–13
- Marzluff JM, Angell T (2005) Cultural coevolution: how human bond with crows and ravens extends theory and raises new questions. J Ecol Anthropol 9(1):69–75. https://doi.org/10.5038/2162-4593.9.1.5
- Marzluff JM, McGowan KJ, Donnelly R, Knight RL (2001) Causes and consequences of expanding American crow populations. In Avian ecology and conservation in an urbanizing world (Eds. J.M. Marzluff, R. Bowman, R. Donnelly), pp. 331–363. Kluwer Academic, Norwell
- Mayer P (2010) Urban ecosystems research joins mainstream ecology Nature: 467: 153, Urban ecosystems research joins mainstream ecology, 7312, https://doi.org/10.1038/467153b
- McKinney ML (2010) Urbanization, biodiversity, and conservation. Bioscience 52:883–890
- McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127(3):247–260. https://doi.org/10.1016/j. biocon.2005.09.005
- McPherson SC, Brown M, Downs CT (2016) Crowned eagle nest sites in an urban landscape: requirements of a large eagle in the Durban metropolitan open space system. Landsc Urban Plan 146:43–50. https://doi.org/10.1016/j.landurbplan.2015.10.004

- Moleón M, Sánchez-Zapata JA, Margalida A, Carrete M, Owen-Smith N, Donázar JA (2014) Humans and scavangers: the evolution of interactions and ecosystem services. Bioscience 64(5):394–403. https:// doi.org/10.1093/biosci/biu034
- Morrison JL, Gottlieb IGW, Pias KE (2016) Spatial distribution and the value of green spaces for urban red-tailed hawks. Urban Ecosyst 19(3):1373–1388. https://doi.org/10.1007/s11252-016-0554-0
- Naoroji R (2006) Birds of prey of the Indian subcontinent. Christopher Helm/AandC Black Publishers Ltd., London
- Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, Dickman CR (2014) The ecological effects of providing resource subsidies to predators. Glob Ecol Biogeogr 24:1–11
- Nilon CH (2011) Urban biodiversity and the importance of management and conservation. Landsc Ecol Eng 7(1):45–52. https://doi.org/10. 1007/s11355-010-0146-8
- Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A (2013) Ecological and evolutionary implications of food subsidies from humans. Ecol Lett 16(12):1501–1514. https://doi.org/10.1111/ele. 12187
- Parker TS, Nilon CH (2012) Urban landscape characteristics correlated with the synurbization of wildlife. Landsc Urban Plan 106(4):316– 325. https://doi.org/10.1016/j.landurbplan.2012.04.003
- Paul S, Nagendra H (2015) Vegetation change and fragmentation in the mega city of Delhi: mapping 25 years of change. Appl Geogr 58: 153–166. https://doi.org/10.1016/j.apgeog.2015.02.001
- Pickett STA, Cadenasso ML, Grovem JM, Nilon CH, Pouyat RV, Zipperer WC, Costanza R (2001) Urban ecological systems: linking terrestrial, ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology Evolution and Systematics 32(1):127–157. https://doi.org/10.1146/annurev. ecolsys.32.081501.114012
- Pinault D (2008) Raw meat skyward: pariah-kite rituals in Lahore. In: Comparative Islamic studies: notes from the fortune-telling parrot: Islam and the struggle for religious pluralism in Pakistan (Ed. D. Paneault). Equinox Publishing Ltd, Bristol, pp 108–121
- R Development Core Team (2009) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org. Accessed 27 Dec 2016
- Sergio F (2003) From individual behavior to population pattern: weatherdependent foraging and breeding performance in black kites. Anim Behav 66(6):1109–1117. https://doi.org/10.1006/anbe.2003.2303
- Sergio F, Newton I (2003) Occupancy as a measure of territory quality. J Anim Ecol 72(5):857–865. https://doi.org/10.1046/j.1365-2656. 2003.00758.x
- Sergio F, Pedrini P, Marchesi L (2003) Spatio-temporal shifts in gradients of habitat quality for an opportunist avian predator. Ecography 26(2):243–255. https://doi.org/10.1034/j.1600-0587.2003.03426.x
- Sergio F, Penteriani V (2005) Public information and territory establishment in a loosely colonial raptor. Ecology 86(2):340–346. https:// doi.org/10.1890/04-0137

- Sharan A (2014) In the city, out of place: nuisance, pollution, and dwelling in Delhi, c. 1850–2000. Oxford University Press, Oxford. https://doi.org/10.1093/acprof.oso/9780198097297.001.0001
- Shochat E, Lerman SB, Anderies JM, Warren PS, Faeth SH, Nilon CH (2010) Invasion, competition, and biodiversity loss in urban ecosystems. Bioscience 60(3):199–208. https://doi.org/10.1525/bio.2010. 60.3.6
- Soh MCK, Sodhi NS, Seoh RKH, Brook BW (2002) Nest site selection of the house crow (*Corvus splendens*), an urban invasive bird species in Singapore and implications for its management. Landsc Urban Plan 59(4):217–226. https://doi.org/10.1016/S0169-2046(02)00047-6
- Sorace A (2002) High density of bird and pest species in urban habitats and the role of predator abundance. Ornis Fennica 79:60–71
- Soulsbury CD, White PCL (2015) Human-wildlife interactions in urban areas: a review of conflicts, benefits and opportunities. Wildl Res 42(7):541–553. https://doi.org/10.1071/WR14229
- Srivastava S (2015) Entangled urbanism: slum, gated community and shopping all in Delhi and Gurgaon. Oxford University Press, Oxford
- Tabachnick BG, Fidell LS (1996) Using multivariate statistics. HarperCollins, New York
- Taneja AV (2015) Saintly animals: the shifting moral and ecological landscapes of North India. Comparative Studies of South Asia, Africa and the Middle East 35(2):204–221. https://doi.org/10. 1215/1089201x-3138988
- Tanferna A, López-Jímenez L, Blas J, Hiraldo F, Sergio F (2013) Habitat selection by black kite breeders and floaters: implications for conservation management of raptor floaters. Biol Conserv 160:1–9. https://doi.org/10.1016/j.biocon.2012.12.031
- United Nations (2014) World urbanization prospects: the 2014 revision highlights. United Nations, New York
- Valone TJ, Templeton JJ (2002) Public information for the assessment of quality: a widespread social phenomenon. Philos Trans R Soc Lond B 357(1427):1549–1155. https://doi.org/10.1098/rstb.2002.1064
- Viñuela J (2000) Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. Behavioural ecology and. Sociobiology 48:333–343
- Wang Y, Bakker F, de Groot R, Wortche H, Leemans R (2015) Effects of urban trees on local outdoor microclimate: synthesizing field measurements by numerical modeling. Urban Ecosystems 18(4):1305– 1331. https://doi.org/10.1007/s11252-015-0447-7
- Warren PS, Lepczyk CA (2012) Beyond the gradient: insights on new work in the avian ecology of urbanizing lands. In: Lepczyk CA, Warren PS (eds) Urban bird ecology and conservation. University of California Press, Berkeley, pp 1–6. https://doi.org/10.1525/ california/9780520273092.003.0001
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York. https://doi.org/10.1007/978-0-387-87458-6

Online Resource 1

Table A1: Environmental variables measured at Black Kite nests and random locations in Delhi (India).

Variable	Description
Nest-area scale:	
Nest substrate	0 = tree; $1 =$ artificial structure (pylon, metal tower, electricity pole, building)
Nest tree species	Species of the nesting tree
DBH (cm) ^a	Diameter of the tree trunk at 1.4 m above the ground
Tree or pylon height (m)	Height of the nesting tree or artificial structure
Nest height (m)	Height of the nest above the ground
Tree arrangement	Categorical variable: $1 = \text{isolated tree/pylon}; 2 = \text{line of trees (e.g. along an avenue}); 3 = \text{parkland}$ (scattered trees with > 5-10 m of open ground between them, typically grassland in urban parks); 4 = woodlot
Woodlot Size (ha)	Size of the woodlot (only for locations classed as 4 above)
Urban scale: landscape structure and composition	
Index of buildings' density	Number of buildings crossed by a 500 m north-south and a 500 m east-west transect crossing each other on the nest/random location
Index of road density	Number of asphalted roads crossed by a 500 m north-south and a 500 m east-west transect crossing each other on the nest/random location
Urban cover	Percentage area covered by built-up structures (buildings, roads, parking lots, or any other impervious surface) within 500 m of the nest/random location
Green cover	Percentage area covered by shrub/tree vegetation within 500 m of the nest/random location
Open habitats	Percentage area free of built-up structures or arboreal vegetation within 500 m of the nest/random location (e.g. water, grassland, cultivated fields, rocky outcrops etc).
Habitat diversity	Shannon-Wiener index of habitat diversity based on the three land cover variables above

Distance to road (m)	Distance to the nearest asphalted road
Distance to water (m)	Distance to the nearest water body
Distance to illegal dump (m)	Distance to the nearest illegal dump (self-created by citizens, not recognized by any local municipality and often present only for a limited period of time)
Distance to landfill (m)	Distance to the nearest, large, authorized refuse dump
Human scale: variables	
characterising human presence, practices and activities	
Historical setting	Categorical variable: $0 =$ more recently built portion of the city (New Delhi); $1 =$ older, more historical portion of the city (Old Delhi) ^b
Hygiene score	Level of sanitation: 1 = clean areas; 2 = areas under poor waste management regimes ^c
Human density	Average number of people walking within 2m of a stationary observer during 5 min at 10 locations randomly plotted within 200 m of the nest/random location ^d
Muslim Density	Estimate of the local density of Muslim inhabitants (see details of calculations in Appendix B)
Access to Muslim subsidies	First component PC1 of a principal component analysis on Muslim density and the proximity to the three closest Muslim colonies

^a For locations on artificial structures, the DBH of the structure was estimated as the value predicted (given its height) by a regression of tree

height on DBH (calculate on tree-sites only).

^bOld Delhi has a higher abundance of old buildings, a higher share of Muslim population and a higher concentration of slaughterhouses and meat selling shops than the more recently built portion of the city. Thus, it may represent a macro-portion of the city with higher availability of

human subsidies (details in Online Resource 2).

^c Categorical variable with two levels: 1 = efficient waste disposal with very scarce or no organic refuse in the streets; 2 = abundant and widespread refuse in the streets throughout the area, either in small frequent piles, in illegal ephemeral dumps, or as individual items scattered a bit of everywhere through all streets (see also Appendix B).

^d Counts were only operated between 10:00-17:00 hrs and avoided during atypical, momentary peak periods of human traffic, such as exits from work or schools, in order to maintain consistency across sites (details in Online Resource 2)

Online Resource 1

Table A2: Mean (\pm 1 SE) estimates of variables measured at 100 Black Kite nests and at 100 randomly chosen locations in Delhi, India. Differences between the two samples were tested by means of t-tests, or χ^2 tests for categorical variables. Symbols: * P < 0.05; ** P < 0.01; *** P < 0.001.

Variable	Nest Sites	Random Locations
Nest-area scale:		
Nest substrate ^{a, b}	88.31 %	80.52 %
DBH (cm) ^b	75.47 ± 2.97	68.86 ± 2.43
Tree or pylon height (m)	14.86 ± 0.72	15.62 ± 0.52
Nest height (m) ^b	11.86 ± 0.63	12.06 ± 0.54
Woodlot size (ha) ***	17.47 ± 2.67	2.89 ± 1.78
Urban scale:		
Index of buildings' density b ***	18.85 ± 1.52	27.45 ± 1.75
Index of road density ^b ***	7.12 ± 5.33	5.33 ± 0.26
Urban cover ^b ***	0.38 ± 0.02	0.53 ± 0.02
Green cover ^b ***	0.28 ± 0.02	0.19 ± 0.01
Open habitats	0.33 ± 0.02	0.28 ± 0.02
Habitat diversity ^b ***	0.96 ± 0.02	0.85 ± 0.02
Distance to road b (m)	81.33 ± 9.72	79.91 ± 8.41
Distance to water $^{b}(m)$	220.32 ± 30.39	275.29 ± 22.62
Distance to illegal dump ^b (m)**	717.08 ± 68.20	435.43 ± 46.82
Distance to landfill ^b (m)	6964.70 ± 318.42	7175.70 ± 355.44
Human scale:		
Historical setting ^c ***	71 %	38 %
Hygiene score ^{b, d} *	66.23 %	50.65 %
Human density ^b ***	12.96 ± 0.97	7.28 ± 0.65
Muslim Density **	32223 ± 2552.13	21296 ± 2231.5
Access to Muslim subsidies ^b **	$0.25 \pm .09$	-0.17 ± 0.1

^a Percent of nest / random locations on trees.

^b Variable that was fitted to the multivariate models of Table A3.

^c Percent of nest / random locations located in Old Delhi.

^d Percentage of locations with poor sanitation.

Online Resource 1

Table A3: Logistic regression (a) and linear mixed models (b, c) testing the effect of

environmental and human variables on nest site selection (a), territory occupancy (b) and

offspring production (c). Plot identity was added as a random factor to all models (see Methods).

Variable	$\mathbf{B} \pm \mathbf{SE}$	Z-test	<i>P-</i> value
a. Dependent variable: nest-site selection ^{a,b}			
(N = 100 nests vs 100 random locations)			
Tree arrangement (tree line) ^c	0.26 ± 0.74	0.35	0.729
Tree arrangement (parkland) ^c	1.65 ± 0.69	2.41	0.015
Tree arrangement (woodland) ^c	2.94 ± 0.86	3.43	< 0.001
Index of road density	0.34 ± 0.11	3.10	0.002
Urban cover	-7.18 ± 2.06	-3.50	< 0.001
Green cover	-1.00 ± 2.88	-0.34	0.731
Human density	0.17 ± 0.05	3.33	< 0.001
Hygiene score	2.38 ± 0.63	3.78	< 0.001
Access to Muslim subsidies	-0.33 ± 1.06	-0.31	0.758
Access to Muslim subsidies * Green cover	8.55 ± 2.87	2.98	0.003
Access to Muslim subsidies * Hygiene score	-2.02 ± 0.80	-2.53	0.011
Intercept	-3.24 ± 1.64	-	-
b. Dependent variable: occupancy d (N = 153 e)			
Tree arrangement (tree line) ^c	0.20 ± 0.28	0.72	0.471
Tree arrangement (parkland) ^c	0.52 ± 0.20	2.56	0.011
Tree arrangement (woodland) ^c	0.35 ± 0.22	1.59	0.111
Access to Muslim subsidies	0.14 ± 0.07	2.11	0.035
Intercept	0.43 ± 0.19	-	-
c. Dependent variable: fledglings produced in			
four years $f(N = 153^{\circ})$			
Tree arrangement (tree line) ^c	0.09 ± 0.36	0.26	0.798
Tree arrangement (parkland) ^c	0.74 ± 0.25	2.95	0.003
Tree arrangement (woodland) ^c	0.23 ± 0.27	0.87	0.384
Access to Muslim subsidies	0.28 ± 0.08	3.51	< 0.001
Intercept	0.03 ± 0.23	-	-

^a Generalised linear mixed model with binomial errors and a logit link function. The model discriminated between 100 kite nests and 100 random locations.

^b Variables presented to the model: Nest substrate, DBH, Tree or pylon height, Nest height, Tree arrangement, Woodlot size, Index of building density, Index of road density, Urban cover, Green cover, Habitat diversity, Distance to road, Distance to water, Distance to illegal dump, Distance to landfill, Hygiene score, Human density, Access to Muslim subsidies, Access to Muslim

subsidies*Urban cover, Access to Muslim subsidies*Green cover, Access to Muslim subsidies*Hygiene score, Human density*Hygiene score (details of the rationale for fitting interactions an be found in the Methods). Variables of Table A1 not presented to the model to avoid collinearity: Open habitats, Historical setting.

- ^c Categorical variable with four levels: 1 = isolated tree/pylon, 2 = line of trees, 3 = parkland, 4 = woodlot.
- ^d Generalised linear mixed model with Poisson errors and a logit link function. The dependent variable is the number of years that a territory was occupied, which ranged from 1 to 4.
- ^e One territory (of the overall sample of 154 territories used for building the nesting habitat selection model) could not be sampled after the first year for logistic reasons (inability to access a private property). Thus, the occupancy and breeding success models were based on a sample of 153 territories, each sampled in all the four years of investigation.
- ^f Generalised linear mixed model with Poisson errors and a logit link function. The dependent variable is the number of young raised to fledging age in four years, which ranged from 0 to 9.

Online Resource 2

Access to human subsidies by Delhi kites: rationale and estimation

In Delhi, kites obtain their main food (meat waste from humans, Kumar et al., 2014) from three major sources: (1) dump (garbage landfill) sites, although these are mainly used by non-breeding kites; (2) roads, especially those with a high density of commercial activities and families, who often dispose their personal waste by leaving it directly in the streets, which may in turn attract potential complementary live prey for kites, such as rodents or pigeons (Kumar et al., 2014, authors' unpublished nest camera-trapping data); (3) direct and indirect effects of religio-cultural practices, such as the higher abundance of meat selling shops and the ritualized-feeding by people who follow Islamic faith in Muslim colonies and in the older establishments of the city (Old Delhi). Thus, because direct, quantitative measurements of such capillary-distributed subsidies would be impossible over such large areas, we considered that proximity to dump sites, local human density in the streets, and religious zoning could be potential surrogates of kite food availability. Therefore, for each nest or random location, we calculated the following variables. (1) First, we measured the distance to the nearest legal or illegal refuse dump site. Such dumps were easily located during our fieldwork on the basis of frequent observation of unauthorized disposal of garbage at certain sites of each plot, where piles of refuse accumulated in evident manners. (2) Second, human traffic and density in the streets was estimated by counting for five minutes the number of people who passed by a stationary observer at 5-10 randomly plotted locations (depending on local conditions, e.g. less points in rural plots with few roads) along the roads within a circle of 200 m centred on each nest or random location. To standardize them as much as possible in relation to human activities, these counts were operated exclusively during working days and between 1000 - 1700 hrs, and halted during unusual events that could have

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biased the estimates (e.g. sudden exit from work or local schools). (3) Third, we interviewed 10 random people in the streets around the nests and random locations about the routine removal of garbage from the local dumps, and integrated it with our own observations of local conditions to create a hygiene index, which classed sites as relatively clean with little litter in the streets and constantly low refuse availability for kites, or as more dirty, with constant presence of large garbage piles in the streets, or in close proximity to stable rubbish dumps (Online Resource 1). (4) Fourth, in the absence of fine-scale data on human population density by religion, we estimated the number of inhabitants of Muslim faith within a 2 km circle centred on each nest or random location in the following manner. First, we extracted the number of Muslim inhabitants for each sub-district of the city, using the 2011 census data

(http://censusindia.gov.in/2011census). Second, we digitized the areal extent of Muslim colonies in each sub-district using Google Earth Pro Imagery and our own ground visits to such colonies. Third, we divided the Muslim population of each sub-district by the area of Muslim colonies within each sub-district to obtain a gross estimate of local Muslim density/unit area, under the assumption that the majority of the Muslim population was concentrated at such "closed" colonies (as supported by well-known and widespread religious ghettoization in India: see Gupta 1998 and Kirmani 2013 for details). Fourth, we multiplied such local density by the actual area of Muslim colonies included in each 2 km-circle, so as to re-adapt the sub-district level Muslim density to the circle around each nest or random location. (5) Finally, we classed locations as placed in the old section of the city (Old Delhi) or within the more recently built up areas (New Delhi). These two categories represented macro-areas under different forms of urbanization history and intensity, configuration, and hygiene, Old Delhi including a large share of Muslim colonies with poor sanitation as well as high concentrations of meat shops.

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Online Resource 3

Mean distance to Muslim colonies for 100 Black Kite nests (black bars) and 100 random locations (white bars) in Delhi (India). The difference between kite nests and random locations was significant for the first and second closest Muslim colony, and marginally significant for the third closest Muslim colony, suggesting over-selection of sites close to multiple sources of ritual subsidies. Symbols: ** P < 0.01; + P < 0.1. Error bars represent 1 SE.



Muslim colony

Online Resource 4

Proportional incidence of tree species among kite nests and random locations in Delhi. There was no significant over-selection or avoidance by kites of main tree species type ($\chi^2 = 6.15$, P = 0.104). The category "Other tree species" incorporated all tree species which occurred less than 5 times among kite nests or random locations and included the following species: Honey mesquite *Prosopis juliflora* (N = 12 for nests and 0 for random locations), Jamun *Syzygium cumini* (10, 1), Semal *Bombax ceiba* (4, 8), Devil's tree *Alstonia scholaris* (3, 4), Indian rosewood *Dalbergia sissoo* (3, 3), Gulmohar *Delonix regia* (2, 0), Siris *Albizia lebbeck* (0, 2), Mango *mangifera indica* (1,1), Cottonwood *Populus gamblei* (1, 1), Dinner Plate tree *Pterospermum acerifolium* (1,0), Monkeypod *Pithecellobium dulce* (0, 1), Unidentified (2, 3).



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Citation: Kumar N, Qureshi Q, Jhala YV, Gosler AG, Sergio F (2018) Offspring defense by an urban raptor responds to human subsidies and ritual animal-feeding practices. PLoS ONE 13(10): e0204549. https://doi.org/10.1371/journal. pone.0204549

Editor: Antoni Margalida, University of Lleida, SPAIN

Received: April 29, 2018

Accepted: August 15, 2018

Published: October 29, 2018

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Data Availability Statement: All relevant data are available on the Oxford Research Archive: https:// doi.org/10.5287/bodleian:KZPgrPVzg (DOI: 10. 5287/bodleian:KZPgrPVzg).

Funding: The project was funded through multiple grants (2013- 2016) by the Raptor Research and Conservation Foundation (Mumbai) <u>http://raptors.</u> <u>net.in/</u> to NK and by the Govt. of India, Ministry of Environment, Forest and Climate Change to YVJ, and NK). N. Kumar's D. Phil (2014-18) at the University of Oxford was funded by the Felix RESEARCH ARTICLE

Offspring defense by an urban raptor responds to human subsidies and ritual animal-feeding practices

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Abstract

There is a growing interest in the behavioural and life history mechanisms that allow animal species to cope with rapidly expanding urban habitats, which impose frequent proximity to humans. A particular case of behavioral bottleneck (i.e. conflicting interests) faced by animals in urban environments is how they will modulate the defence of their offspring against the potential danger represented by humans, an aspect that has received scarce research attention. We examined the nest defense against humans by a dense breeding population of a raptor, the Black Kite Milvus migrans, within the megacity of Delhi (India). Here, kites live on a diet dominated by human waste and meat offered through religiously motivated bird feeding practices. Nest defense levels increased with the number of offspring, and with the progression of the breeding season. Defense also intensified close to ritual-feeding areas and with increasing human waste in the streets, suggesting synergistic effects of food availability, parental investment, personality-boldness and habituation to humans, with consequent attenuation of fear. Thus, the behavioural response to a perceived threat reflected the spatial mosaic of activity of humans in the city streets, their cultural practices of ritualfeeding, and their waste-management. For synurbic species, at the higher-end spectrum of adaptation to an urban life, human cultural practices and attitudes may well be the most defining dimensions of their urban niche. Our results suggest that, after initial urban colonization, animals may continue to adapt to the typically complex, heterogeneous environments of cities through fine-grained behavioural adjustments to human practices and activities.

Introduction

Rapid, worldwide urbanization is raising interest in urban ecology and in the ways animals adapt to novel and burgeoning urban environments [1]. In particular, behavioural mechanisms that mediate such adaptation remain an under-researched topic [2, 3], with current



Scholarship Trust and Somerville College (https:// www.some.ox.ac.uk: Discretionary Grant 2017). Funding for travelling and fieldwork by F. Sergio was afforded by Project CGL2015- 69445-P of the Spanish Ministry of Economy and Competitiveness.

Competing interests: The authors have declared that no competing interests exist.

knowledge mostly limited to a handful of species that have only recently colonized or are in the process of capitalizing on urban environments e.g. [2, 4, 5]. Furthermore, these species have typically been studied in biogeographic regions with a long history of wildlife persecution by humans, whose proximity is frequently seen as a potential obstacle for urban colonization e.g. [6, 7]. For example, many studies have focused on flight initiation distances (FID) to explore how behavioural characteristics or personality features may allow certain individuals to better cope with proximity to humans in highly anthropogenic environments [8–12].

A different scenario may be represented by those 'synurbic' species [13] that have lived within human settlements for centuries. These species often show limited fear of humans and sometimes even directly exploit them, as in the case of many populations dependent on carrion or garbage in traditional human societies which, often because of the ecosystem services they provide, do not persecute them e.g. [14]. Information on the behavioural responses to humans by these urban specialists would complete our current picture of adaptation to a rapidly urbanising world and offer insights into the range of behavioural strategies potentially employed by urban wildlife to cope with a constant high proximity to humans [15, 16].

One particularly interesting case of behavioural bottleneck (i.e. conflicting interests) faced by animals in urban environments is how to modulate their defence of young in a fixed nest or den against the potential danger presented by humans. Such modulation is especially relevant for large vertebrates armed with potentially dangerous weaponry and thus theoretically capable to drive humans away. This scenario is more complex than the one examined in studies of flight initiation distance, because the fitness investment at stake (the offspring) is not mobile and cannot be fully controlled by the animal (e.g. by fleeing). Thus, it may be particularly informative of the extent to which urban animals perceive humans as a threat, how much risk they are willing to take to defend their parental investment, and how this may vary along a range of urban configurations and human attitudes towards wildlife. To our knowledge, few studies have examined such aspects and most of them have focused essentially on the comparison of behavioural traits between urban and rural individuals (review in [2, 7]). While this comparison renders important information on trait expression associated with the colonization of urban environments, it assumes that all individuals that colonized a city adopted the same behavioural strategies [16]. However, urban environments are often highly heterogeneous mosaics with marked variation in physical structure or human density [17, 18], to which animals are likely to respond, potentially selecting for a more complex array of behavioural strategies in urban animals than has thus far been recognized.

To explore these aspects, here we examine patterns of nest defense against humans by a synurbic raptor, the Black Kite Milvus migrans, which exploits humans for food in a megacity (Delhi, India) that incorporates a wide range of urban conditions, human densities and ritualized animal-feeding practices. The Black Kite (hereafter kite) is a medium-sized opportunistic raptor, widely distributed throughout Eurasia, Africa and Australia, and considered the most successful raptor in the world. In India, the native, resident subspecies M. m. govinda is synurbic (sensu [13]], occurring almost exclusively in close association with humans in towns and cities [19]. In Delhi, kites breed on both trees and artificial structures (pylons, towers), sometimes forming loose colonies and locally reaching extremely high densities, thanks to the exploitation of human food 'subsidies' facilitated by inefficient refuse disposal and by religious kite-feeding practices [20, 21]; (see Study area below). In particular, the relationship between kites and humans in Delhi is dual: on one hand, kites depend on humans for food and thus over-select breeding sectors in the city close to ritual-feeding sites, and with a high density of humans and of their garbage in the streets [20]. On the other hand, people sometimes rob or destroy kite nests to collect nestlings for the illegal bird trade, or to remove dangerous nest materials from electricity pylons, telephone towers or light poles during maintenance

operations [22]. Thus, humans approaching a nest can be perceived by kites as a potential threat to their offspring, soliciting a defense response.

We feel that this represents a particularly interesting case study because: (1) Delhi kites directly exploit humans for food, by accessing their waste or by grabbing meat offered to them by people through religious, ritual feeding practices. Thus, they frequently come into close contact with humans, which may affect their perception and fear of humans. (2) These offerings and garbage disposal practices vary dramatically through the city (see Study area below), implying that different kites may experience and perceive people in different ways through the urban mosaic. (3) As medium-sized raptors armed with sharp talons and high aerial agility, kites are potentially well capable to inflict injury on people and drive them away from their nest-area. However, (4) much of the mortality experienced by kites is still of anthropogenic origin [22], implying a delicate trade-off between the need to come close to humans for feeding but avoid them or repel them in the appropriate context to ensure their own or their offspring safety. Given all the above, when faced with people approaching their nest, kites will need to take a quick defense-tactic decision, which may reflect these conflicting pressures. Furthermore, the balance of these pressures may change through the complex mosaic offered by this megacity of 16 million people. In particular, because ready access to dense Muslim colonies rich in ritual-subsidies is considered a key resource in this population (see [20, 21] and Study area below), we hypothesized that it could alter the profitability for kites of hygiene levels, green cover or built-up cover, ultimately affecting the defense-value of the offspring.

Materials and methods

This research is part of a larger and long-term study on the demography of Black Kites in Delhi and has received bioethical approval by the Training, Research, and Academic Council (TRAC) of the Wildlife Institute of India, Dehradun. The project took all precautions to ensure researcher and animal safety. The study did not involve human participants other than the research team.

Study area

Delhi is a megacity of more than 16 million inhabitants, currently covering an area of 1500 km² and in constant, rapid expansion [23]. It is polycentric and heterogeneous, with a multitude of juxtaposed urban configurations, which make it difficult to establish a linear urbanrural gradient. Two aspects of Delhi are important in determining the food availability and habitat quality for kites [20]. First, large portions of the city are characterized by poor solid waste management, which affords food to kites in the form of carrion or refuse, and its associated prey-fauna (e.g. rodents, pigeons etc.). Secondly, many people (primarily in Muslim settlements) engage in the centuries-old religious practice of feeding meat scraps to kites (hereafter termed "ritualized-feeding") typically offered by throwing meat into the air for the birds to catch. These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries [24, 25]. Thus, waste management issues common to all communities, and cultural rituals which are more specific to some, generate spatial heterogeneity in the potential food availability for kites [20].

Field procedures

We systematically surveyed kite nests during 2013–2016 at 24 plots of 1 km², which were randomly stratified within Delhi (1500 km²) so as to cover all its possible urban settings, from semi-natural to extremely built-up sites (details in [21]). This resulted in a sample of 101 nests, each from a different territory, used at least once for breeding between 2013 and 2016. Nests were checked every 7-10 days until the chicks were at least 45 days old, in order to estimate the number of young raised to fledging (chicks fledge when about 48 days old) (see [21] for further details of nest checks and surveys). During each nest check, we assessed the intensity of offspring defense by the parents against our own human intrusion as follows. During each visit, a team consisting of a tree-climber (always the same for each nest) and one or two accompanying observers positioned themselves at a point from where the kite nest was in clear sight. The point was chosen so as to be clearly visible to the parent kite perched in the nest area. The team then walked slowly towards the nest. Once under the nest, we observed the behaviour of the adults for 20 minutes while the tree-climber reached the nest and checked its content. We classified the intensity of defense according to the following ordinal score: (score 0) the kite remains perched at a distance (> 20 m) or flies far away, either silently or after alarm-calling a few times; (score 1) it flies directly above the field-team in an excited manner while calling repeatedly, or perches close-by (within 20 m) and alarms continuously, or perches within a few metres of the climber (within the same nesting tree); and (score 2) it repeatedly divebombs at the climber and ground-team, it may even stoop among tree-branches or electricity wires, or perch a few metres from a team-member and then stoop again, sometimes hitting or scratching with open talons, while continuously alarm-calling. Thus, progressively higher scores were associated with higher costs and risks for the defending kite, including (a) increases in energy costly activities, such as alarm-calling or flapping flight, and (b) increases in potential risks, such as injuries while manoeuvring through the canopy or overhead electric wires. Throughout, the defense score refers to the maximum intensity of defense shown by either of the partners of each pair. This was justified by the fact that: (1) kites are monomorphic, making it impossible to distinguish males from females; and (2) no difference in defense levels was noticed between the two partners of a pair (if one attacked, the other also attacked, while if one remained quietly perched, the other did the same). All defense ratings were carried out between 08:00 and 18:00 hrs (local time) avoiding unusual weather conditions (e.g. rain, or excessive heat).

Predictors of offspring defense

To investigate how kite defense varied across the Delhi mosaic of urban structure, human densities and practices, we measured a series of environmental, urban and human variables previously found to be important components of habitat quality and food availability in this population [20]. These variables are detailed in Table 1 and were devised so as to characterise: (1) the timing, context and characteristics of the defense trial (e.g. number of people in the visiting team, number of previous visits to a target nest); (2) the breeding stage, social setting (intraspecific spacing) and content of the nest during the trial (e.g. number of offspring to be defended); (3) the physical features of the nest and its immediate surroundings (e.g. its location within a hedge, park or continuous woodland); (4) the urban landscape structure around the nest (e.g. local road density or extent of impervious surfaces in the surroundings); and (5) direct and indirect estimates of human activities and practices (e.g. access to dense Muslim colonies for reasons stated above, efficiency of waste management, or human density). Further details of the recorded variables and their ecological rationale are given in Table 1 and in [20].

In particular, a key variable in our previous analyses on the predictors of kite site selection, occupancy and breeding performance was the ease of access to dense Muslim colonies, which provide abundant food supplies in the form of ritual subsidies [20]. More specifically, we previously showed that Delhi kites over-selected for breeding sites closer than available to the 1st, 2nd and, possibly, 3rd nearest Muslim colony (see [20] for details). Thus, to provide a comprehensive measure that integrated the proximity to the three nearest Muslim colonies with their

Variable	Description, rationale for use and predicted effect
Julian date	Julian date of nest inspection. Earlier laying raptors are often older or higher quality individuals with higher parental investments and were thus expected to be more aggressive [52].
Breeding stage	The breeding cycle was divided into five main stages: (1) pre- incubation; (2) incubation (3) nestlings younger than 15 days; (4) nestlings of 15–30 days; (5) pre-fledging: 30–48 days old nestlings; (6) post-fledging. We expected defense to vary by stage because avian nest defense often varies through the breeding season in conjunction with the growing survival probabilities of the offspring e.g. [33–35].
Previous visits	Number of previous nest checks by the research team. This variable was fitted to control for potential habituation or reinforcement of aggressiveness by repeated sampling of the same pair [53].
Team size	Number of people in the research team (2 or 3). This was fitted to examine the impact of the number of intruders on defense, if any.
Number of onlookers	Number of people (not belonging to the field-team) within 20 m of the nest during the defense trial. This was fitted to examine the impact of the number of onlookers on defense, if any.
Number of offspring	Number of eggs or chicks in the nest at the time of the defense trial. We expected higher aggression by pairs with larger parental investments, as found in some previous studies e.g. [33–35].
NND5 (m)	Mean distance to the five closest kite neighbors. This variable focused on the impact of local, spatial arrangement on defense intensity. We expected higher defense under more crowded conditions (i.e. at higher quality, more attractive sites, which may entail higher parental investments).
Territories within 200 m	Number of territories occupied within 200 m of the target nest. This variable focused on the impact of local density on defense intensity. We expected higher defense levels at higher local densities (i.e. at higher quality, more attractive sites, which may entail higher parental investments).
Colony size	Number of nests within the kite colony. We expected larger colonies to be more attractive to individuals of a semi-social species, or to be associated with higher vigilance and larger food supplies, leading to a higher motivation for defense.
Tree arrangement	Categorical variable: 1 = isolated tree/pylon; 2 = line of trees (e.g. along an avenue); 3 = parkland (scattered trees with $> 5-10$ m of open ground between them, typically grassland in urban parks); 4 = woodlot. These habitat configurations are known to be differentially attractive to Delhi kites [20] and were fitted in order to investigate links between habitat quality, urban landscape configuration and defense intensity.
Balcony	Categorical variable: 0 = absence, 1 = presence of a balcony within 20 m of the nest. We predicted that pairs in such close and constant contact with humans could show higher aggressiveness through habituation and loss of fear.
Index of road density	Number of asphalted roads crossed by a 500 m north-south and a 500 m east-west transect crossing each other on the nest. Delhi kites over-select areas with more extensive road networks, which are one of their main foraging habitats [20]. Thus, we expected defense-levels to increase with road density.
Urban cover	Percentage area covered by built-up structures (buildings, roads, parking lots, or any other impervious surface) within 500 m of the nest. Urban and tree cover were fitted to investigate links between offspring defense and urban landscape configurations. Urban cover was also fitted as a quadratic effect to test the "intermediate disturbance hypothesis" commonly proposed in the urban ecology literature [54], by which the favourability of urban ecosystems to wildlife peaks at intermediate levels of the urbanization gradient.
Green cover	Percentage area covered by shrub/tree vegetation within 500 m of the nest. Urban and tree cover were fitted to investigate links between offspring defense and urban landscape configurations.
Hygiene score	Level of sanitation: $1 =$ clean areas; $2 =$ areas under poor waste management regimes ^a . The level of street sanitation is an important component of habitat quality for this population [20]. We expected higher aggression at sites with lower sanitation because of frequent exposure to humans and because larger food supplies may imply larger broods and thus higher parental investments.

Table 1. Variables measured during nest defense trials conducted at Black kite nests within the city of Delhi (India).

(Continued)

Table 1. (0	Continued)
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Variable	Description, rationale for use and predicted effect
Human density	Average number of people walking within 2m of a stationary observer during 5 min at 10 locations randomly plotted within 200 m of the nest ^b . Delhi kites over-select sites with intense human activity in the streets, leading to more food in the form of human refuse [20]. We expected defense-levels to increase with human density in the streets because of frequent exposure to humans and because larger food supplies may imply larger broods and thus higher parental investments.
Access to Muslim subsidies	First component (PC1) of a principal component analysis on Muslim density and on the proximity to the three closest Muslim colonies (see <u>Methods</u>). Muslim subsidies are one of the main food resources for Delhi kites [20, 21] and ready access to them was predicted to boost offspring-defense because of frequent exposure to humans and because larger food supplies may imply larger broods and thus higher parental investments.

^a Categorical variable with two levels: 1 = efficient waste disposal with very scarce or no organic refuse in the streets; 2 = abundant and widespread refuse in the streets throughout the area, either in small frequent piles, in illegal ephemeral dumps, or as individual items scattered a bit of everywhere through all streets [20].

^b Counts were only operated between 10:00–17:00 hrs and avoided during atypical, momentary peak periods of human traffic, such as exits from work or schools, in order to maintain consistency across sites [20].

https://doi.org/10.1371/journal.pone.0204549.t001

human population density (under the assumption that higher rates of refuse and ritualizedfeeding should occur in more densely-populated Muslim colonies), we extracted the first component of a PCA [26] run on these four aforementioned variables. Its PC1 (hereafter "access to Muslim subsidies") explained 65% of the variance and had a high positive loading on Muslim population density and high negative loadings on the distance to the 1st, 2nd and 3rd closest Muslim colonies. Thus, it provided an increasing index of access to abundant "Muslim subsidies".

Statistical analysis

We employed a linear mixed effect ordinal regression (cumulative-link mixed effect model), [27, 28] through package "ordinal" [29] to examine the effect of environmental, urban and human variables on the ordinal score of offspring defense. The ordinal regression was run on 657 defence trials conducted at 101 unique nesting territories. Because territories were sampled repeatedly, and because territories within the same plot were closer and thus potentially more similar than territories sampled in different plots, we fitted as a random effect territory identity nested within plot identity and year, so as to control for pseudoreplication and spatial autocorrelation [30]. To reduce collinearity and the number of variables presented to the logistic regression, we considered pairs of strongly inter-correlated variables (r > 0.60) as estimates of a single underlying factor, and only retained for analysis the one estimated to be more biologically important for the study organism.

To explore further the potential link between defense intensity and subsequent breeding benefits, we related the eventual number of fledged young to the intensity of defense during incubation (i.e. about two months before fledging) by means of a linear mixed model, again with territory identity nested within plot identity and year as a random term.

All multivariate models were built through a backward stepwise procedure following Zuur et al. [30]: all explanatory variables were fitted to a maximal model, extracted one at a time from the maximal model, and the associated change in model deviance was assessed by the significance of a likelihood-ratio test; the procedure was repeated until we obtained a final model which only included significant variables [30]. To avoid over-parameterization, we ensured never to fit more than N/3 variables to each maximal model, where N is the sample size of the

analysed dataset [31]. Interactions were fitted only when we had a priori hypotheses about their potential effect, based on our field observations and knowledge of the population. To explore the possibility of curvilinear relationships, we fitted continuous variables as linear and also as quadratic terms. Explanatory variables were fitted as standardized Z-scores because of their different measurement units and in order to better evaluate their relative importance [32]. Model assumptions were checked by investigating QQ plots, histograms of residuals, and plots of standardized and normalized residuals against fitted values and against explanatory variables [30, 31]. All mixed models were implemented in R.3.4.3 [33], all tests are two-tailed, statistical significance was set at < 0.05, and all means are given \pm 1 SE.

Results

Several variables entered the mixed model ordinal regression (Table 2). First, defense intensity increased progressively along the breeding cycle and then declined in its final stages, especially after the young fledged from the nest (Fig 1A). Second, defense levels increased with the number of offspring in the nest (Fig 1B). Third, the interaction of Access to Muslim subsidies and Hygiene score was also significant (Table 2 and Fig 1C): under conditions of poor sanitation,

Table 2. Cumulative-link mixed effect ordinal regression (a) testing the effect of environmental, urban and human variables on the ordinal intensity of offspring defense; and (b) linear mixed effect model testing the effect of intensity of offspring defense in incubation on eventual fledgling production.

Variable	ß ± SE	Z-test	P- value
a. Dependent variable: Intensity of defense (N = 657) ^{a,b}			
Breeding Stage (incubation)	1.11 ± 0.8	1.39	0.164
Breeding Stage (small nestling)	3.11 ± 0.82	3.81	< 0.001
Breeding Stage (large nestling)	3.83 ± 0.8	4.78	< 0.0001
Breeding Stage (pre-fledging)	2.34 ± 0.76	3.07	0.002
Breeding Stage (post-fledging)	0.71 ± 0.97	0.73	0.463
Offspring number	1.61 ± 0.33	4.81	< 0.0001
Access to Muslim subsidies	-6.23 ± 2.01	-3.1	0.001
Hygiene score	3.25 ± 1.01	3.24	0.001
Access to Muslim subsidies * Hygiene score	4.5 ± 2.02	2.22	0.026
Green cover	-1.65 ± 0.68	-2.4	0.016
Urban cover	-3.69 ± 1.62	-2.28	0.022
Urban cover ^2	3.20 ± 1.67	1.9	0.057
b. Dependent variable: fledglings produced ^c (N = 103)			
Intensity of defense (during incubation)	0.28 ± 0.12	2.27	0.023
Intercept	-0.36 ± 0.17	-	-

^a Cumulative link mixed model with a logit link function, based on N = 657 defense trials from 101 independent territories. The dependent variable is the ordinal score of offspring defense intensity. Territory-identity nested within plot-identity and year was fitted as a random factor.

^b Variables presented to the model: Julian date, Team size, Number of onlookers, Previous visits, Breeding Stage, Offspring number, NND5, Territories within 200 m, Tree arrangement, Balcony, Index of road density, Urban cover, Green cover, Hygiene score, Human density, Access to Muslim subsidies, Access to Muslim subsidies*Hygiene score, Access to Muslim subsidies*Urban cover, Access to Muslim subsidies*Green cover (the rationale for fitting interactions can be found in the Methods).

^c Generalised linear mixed model with Poisson errors and a logit link function, based on N = 103 defense trials from 60 independent territories sampled during incubation. The dependent variable is the number of young raised to fledging stage. Territory-identity nested within plot-identity and year was fitted as a random factor.

https://doi.org/10.1371/journal.pone.0204549.t002





Fig 1. The intensity of offspring defense by kites in Delhi (India) varied with: panel (a) the stage of the breeding cycle; panel (b) the number of offspring (eggs and/or chicks) in the nest at the time of the defense trial; and panel (c) the interaction between access to Muslim subsidies and the amount of human waste in the streets (the black circles and the solid line indicate breeding sites with poor street sanitation, while the white quadrats and dotted line portray cleaner sites with less refuse in the streets). In panel c, Access to Muslim subsidies is shown above and below the median value ("high" and "low", respectively) for clarity of presentation. Error bars represent ± 1 SE.

https://doi.org/10.1371/journal.pone.0204549.g001

defense levels increased more steeply with access to dense Muslim colonies than under cleaner conditions, suggesting that low sanitation and ready access to Muslim subsidies acted in concert, i.e. synergistically affecting aggressiveness. Fourth, defense intensity declined with the green cover and was minimum at intermediate levels of built-up cover (Table 2A).

Finally, the number of fledglings produced by a pair was positively related to the defense intensity recorded for the same pair about two months earlier during incubation (Table 2B and Fig 2).





https://doi.org/10.1371/journal.pone.0204549.g002

Discussion

Kite defense levels progressively increased through the breeding cycle and reflected the number of offspring in the nest during each trial. These results confirmed those of several earlier studies e.g. [34-36] and suggested that parents tuned their defense response in relation to their parental investment, i.e. on the quantity and future survival prospects of their offspring, which increased through the breeding cycle. The fact that defense intensity early in the season predicted eventual young production months later, by the end of breeding, implied three nonexclusive possibilities: (1) parents could estimate the eventual likelihood of breeding success early in the season and set their defense accordingly; (2) aggressive nest defense lowered predation rates at the nest, with consequent benefits for young production; or (3) high quality individuals (e.g. healthier, or larger) were simultaneously more aggressive and better breeders, generating a positive association between two parameters separated by months in time. For example, kites that were more aggressive against humans could potentially be more aggressive against other more common nest predators such as crows or monkeys [21]. In support of this idea, in another study, nest defense by a falcon was experimentally shown to lower nest predation rates by corvids [35]. The above mix of associative and causative mechanisms produced results that are typical of avian nest defense studies e.g. [37, 38], suggesting that life in an urban setting did not disrupt the typical links between behavioural traits and vital rates found in avian populations.

More notably, despite constant close exposure to people, kite defense suggested that humans were not perceived as a neutral component of the urban landscape, but rather as a potential danger when they approached a nest. This implied a capability by kites to discriminate human attitudes and adjust their behaviour in a context-dependent manner, approaching people to very close quarters for feeding but fleeing and sometimes even attacking them when defending their offspring. Furthermore, defense levels varied through the city in relation to cultural ritual-feeding practices, refuse management and landscape composition. In particular, defense intensity was higher at sites that combined ready access to dense Muslim colonies (where kites are fed by humans by tossing meat-scraps at very close quarters) with poor sanitation (which promotes frequent feeding on anthropogenic waste close to people, e.g. at ephemeral garbage dumps also used by poor rag pickers digging for useful materials). This spatial association could be the result of three non-exclusive mechanisms: (a) frequent and reiterated, close contact with humans may have lowered fear, thus enhancing boldness and aggression; (b) sites close to ritual-feeding areas or with poor sanitation are over-selected by kites and thus likely occupied by higher quality individuals with higher parental investments [20], leading to higher defense intensity; and (c) bolder individuals may be more likely to withstand constant close proximity to humans and a bolder temperament is associated with greater aggression in some species e.g. [39]. Thus, individual quality, personality, habituation and motivation may have generated a spatial association between a behavioural strategy and a human cultural landscape, thus contributing to the growing appreciation of the importance of human cultural geographies for urban ecology e.g. [40-43].

While the exact mechanism remains uncertain, the behavioural response of kites to a perceived threat was finely tuned on the spatial arrangement of human activities and ritual practices, their consequent attitudes towards the birds, and their waste management organization. In turn, this would create a dynamic behavioural landscape, reflecting the underlying urban mosaic of resources, structures and human attitudes, to which kites will necessarily have to adapt and respond, as shown for species that colonized urban environments more recently [5].

The fact that aggression peaked at close human proximity suggested that close coexistence and habituation to people led to a loss of fear and heightened boldness towards humans, rather than an enhanced capability to avoid them by keeping a "low profile" or learning to ignore them. Such dynamics may have been further favoured by the generally positive, religiously-based attitudes of Indian people towards wildlife, as reported by several studies e.g. [44–46].

Overall, these results confirm and extend earlier findings of more aggressive offspring defense by urban than rural individuals of a given species e.g. [47–49], suggesting that the route to close coexistence with humans is often accompanied by fine-grained, context-dependent strategies and trade-offs, rather than evolution of "blind tolerance" and indifference towards human activities [50]. In this sense, most animals making frequent contact with humans (through colonization of urban habitats, or through peri-urban encroachment) will likely need to develop cognitive capabilities and behavioural tactics that will enable them to exploit humans and cope with their omnipresent disturbance rather than learning to ignore them, in order to attain long-term coexistence e.g. [10, 51]. In turn, acquisition of such traits will likely be shaped by a two-way interaction between human perceptions, attitudes and practices on one part and daily experience and habituation to humans on the part of the animal. For synurbic species, like kites, at the high end of the spectrum of adaptation to an urban life, the above cited interaction may lead to behavioural and demographic traits fine-tuned not only on urban physical structures, but also on human cultural practices and attitudes, which for many species may become the most important, defining dimensions of their urban niche.

To date, most studies of animal behavioural responses to urbanization have focused on the comparison between urban and rural individuals, in order to draw inferences on the characteristics that enable or mediate the colonization of highly anthropogenic urban environments e.g. [7, 9, 10]. Here, we show that marked heterogeneity in behavioural responses to humans also continue to exist within cities and after centuries of initial urban colonization, suggesting further fine-tuning of behavioural traits on specific dimensions of the urban environment. In this sense, the urban-rural comparison does not target the end-result of colonization, but rather defines only the beginning of a hierarchical process of adaptation to humans, who are increasingly concentrated in cities. Thus, more research is needed on the fine-grained adjustments to urban structure and human culture by animals that are already in their mature stage of adaptation to an urban life.

Acknowledgments

We are grateful to Ben Sheldon, Chris Perrins, Tommaso Pizzari, Ujjwal Kumar, and the Director, Dean and research coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. We thank Drs. A. Margalida, W. Cresswell and two anonymous reviewers for helping us to improve a first draft of the manuscript. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Delhi Transport Corporation, Civic bodies of the Government of NCT of Delhi helped with legal permits, and the Director of the National Zoological Park of New Delhi gave access to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We express our most heartfelt gratitude to all the volunteers of the "Black Kite Project Group" from the University of Delhi (Sri Venkateswara and Deshbandhu Colleges), especially U. Gupta, H. Malhotra, A. Singh, P. Kumar, H. Singh, U. Nair and M. Singh, who provided essential field help, enthusiasm and cooperation in the environmental education of locally assembling crowds of curious people. Special thanks to our field assistants Laxmi Narayan, Prince Kumar and Poonam, who were the backbone of the field team. Finally, thanks to all the landowners, managers and government officials who patiently cooperated with our constant requests of access. We are thankful to the Publication Fee Assistance for financial support towards the publication of this manuscript.

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References

- 1. McDonnell MJ, Hahs AK. Adaptation and adaptedness of organisms to urban environments. Annual Review of Ecology, Evolution, and Systematics. 2015; 46: 261–280.
- Miranda AC, Schielzeth H, Sonntag T, Partecke J. Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? Global Change Biology. 2013; 19:2634–2644. <u>https://doi.org/10.1111/gcb.12258</u> PMID: 23681984
- 3. Hahs AK, Evans KL. Expanding fundamental ecological knowledge by studying urban ecosystems. Functional Ecology. 2015; 29:863–867. https://doi.org/10.1111/1365-2435.12488
- Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ. Avian productivity in urban landscapes: a review and meta-analysis. Ibis. 2009; 151(1):1–18. https://doi.org/10.1111/j.1474-919X.2008.00899.x
- Evans KL, Hatchwell BJ, Parnell M, Gaston KJ. A conceptual framework for the colonisation of urban areas: the blackbird *Turdus merula* as a case study. Biological Reviews. 2010b; https://doi.org/10.1111/ j.1469-185x.2010.00121.x
- Smart J, Amar A, Sim IM, Etheridge B, Cameron D, Christie G, Wilson JD. Illegal killing slows population recovery of a re-introduced raptor of high conservation concern–The red kite *Milvus milvus*. Biological Conservation. 2010; 143:1278–1286. https://doi.org/10.1016/j.biocon.2010.03.002
- Lowry H, Lill A, Wong BBM. Behavioural responses of wildlife to urban environments. Biological Reviews 88:537–549. 2013; https://doi.org/10.1111/brv.12012 PMID: 23279382
- Blumstein DT. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. Animal Behaviour. 2006; 71:389–399. https://doi.org/10.1016/j. anbehav.2005.05.010
- 9. Møller AP. Flight distance of urban birds, predation, and selection for urban life. Behavioral Ecology and Sociobiology. 2008; 63:63–75. https://doi.org/10.1007/s00265-008-0636-y
- Carrete M, Tella JL. Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. PLoS One. 2011; 6(4): e18859. <u>https://doi.org/10.1371/journal.pone.0018859</u> PMID: 21526193
- 11. Clucas B and Marzluff JM. Attitudes and actions toward birds in urban areas: human cultural differences influence bird behavior. Auk. 2012; 129:8–16. https://doi.org/10.1525/auk.2011.11121

- Sprau P, Dingemanse NJ. An Approach to Distinguish between Plasticity and Non-random Distributions of Behavioral Types Along Urban Gradients in a Wild Passerine Bird. Frontiers in Ecology and Evolution. 2017; https://doi.org/10.3389/fevo.2017.00092
- Francis RA, Chadwick MA. What makes a species sunurbic? Applied Geography. 2012; 32(2):514– 521.
- Gangoso L, Agudo R, Anadón JD, Manuel de la R, Suleyman AS, Porter R, et al. Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem services providers. Conservation Letters. 2012; 6:172–179. https://doi.org/10.1111/j.1755-263x.2012.00289.x
- **15.** Kark S, Iwaniuk A, Schalimtzek A, Banker E. Living in the city: can anyone become an urban exploiter'? Journal of Biogeography. 2007; 34:638–651. https://doi.org/10.1111/j.1365-2699.2006.01638.x
- Evans KL, Chamberlain DE, Hatchwell BJ, Gregory RD, Gaston KJ. What makes an urban bird? Global Change Biology. 2010a; 17:32–44. https://doi.org/10.1111/j.1365-2486.2010.02247.x
- Grimm NB, Grove JM, Pickett ST, Redman CL. Integrated Approaches to Long-Term Studies of Urban Ecological Systems. BioScience. 2000; https://doi.org/10.1007/978-0-387-73412-5_8
- Lepczyk CA, Aronson MFJ, Goddard MA, Lerman SB, Malvor JS. Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. Bioscience. 2017; 67(9):799–807. <u>https://doi.org/10.1093/biosci/bix079</u>
- 19. Naoroji R. Birds of prey of the Indian subcontinent. Om Books International, New Delhi, India; 2007.
- Kumar N, Gupta U, Jhala YV, Qureshi Q, Gosler AG, Sergio F. Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools. Urban Ecosystems. 2018; 21:339–349. https://doi.org/10.1007/s11252-017-0716-8
- Kumar N, Mohan D, Jhala YV, Qureshi Q, Sergio F. Density, laying date, breeding success and diet of Black Kites *Milvus migrans govinda* in the city of Delhi (India). Bird Study. 2014; 61:1–8. <u>https://doi.org/ 10.1080/00063657.2013.876972</u>
- Kumar N. A study of resource selection by Black Kites Milvus migrans in the National Capital Region. M.Sc. Thesis submitted to Wildlife Institute of India; Saurashtra University. Rajkot. Gujarat; 2013.
- 23. Census organization of India [Internet]. Census of India; c2011 [cited 25 Feb 2018]. Available from: http://censusindia.gov.in/2011census.
- Pinault D. Raw meat skyward: Pariah-kite rituals in Lahore. In: Comparative Islamic studies: notes from the fortune-telling parrot: Islam and the struggle for religious pluralism in Pakistan (Ed. D. Pinault), pp. 108–121, Equinox Publishing Ltd, Bristol, CT, USA; 2008.
- 25. Taneja AV. Saintly animals: the shifting moral and ecological landscapes of North India. Comparative Studies of South Asia, Africa and the Middle East. 2015; 35:204–221.
- 26. Tabachnick BG, Fidell LS. Using multivariate statistics. HarperCollins, New York, USA; 1996.
- Hedeker D, Gibbons RD. A Random-effects ordinal regression model for multilevel analysis. Biometrics. 1994; 50:933–944. PMID: 7787006
- 28. Agresti A. Analysis of ordinal categorical data, 2nd edn. Wiley, New York, USA; 2010.
- Christensen RHB [Internet]. Regression Models for Ordinal Data [R package ordinal version 2015.6– 28]. In: The Comprehensive R Archive Network; c2015 [cited 27 Sept 2017]. Available from: http://cran. r-project.org/web/packages/ordinal/.
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. Mixed effects models and extensions in ecology with R. Springer, New York, USA; 2011.
- 31. Crawley MJ. The R book. Wiley Press, Chichester, UK; 2013.
- Grueber CE, Nakagawa S, Laws RJ, Jamieson IG. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 2011; 24: 699–711. https://doi.org/10.1111/j.1420-9101.2010. 02210.x PMID: 21272107
- R Development Core Team [Internet]. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL; c2009 [cited 27 Sept 2018]. Available from: http://www.R-project.org
- Hakkarainen H, Korpimäki E. Nest defence of Tengmalm's owls reflects offspring survival prospects under fluctuating food conditions. Animal Behaviour. 1994; 48:843–849.
- **35.** Sergio F, Bogliani G. Nest Defense as Parental Care in the Northern Hobby (*Falco subbuteo*). The Auk. 2001; 118:1047. https://doi.org/10.1642/0004-8038(2001)118[1047:ndapci]2.0.co;2
- Møller AP, Nielsen JT. Parental defense of offspring and life history of a long-lived raptor. Behavioral Ecology. 2014; 25:1505–1512. https://doi.org/10.1093/beheco/aru130
- Montgomerie RD, Weatherhead PJ. Risks and rewards of nest defence by parent birds. Q Rev Biol. 1988; 63: 167–187.

- Redondo T. Avian Nest Defence: Theoretical Models and Evidence. Behaviour. 1989; 111:161–195. https://doi.org/10.1163/156853989x00646
- Evans JE, Boudreau K, Hyman J. Behavioural syndromes in urban and rural populations of song sparrows. Ethology. 2010; 116: 588–595.
- Alberti M. Advances in urban ecology: integrating humans and ecological processes in urban ecosystems. Springer, New York; 2008.
- 41. Forman RTT. Urban ecology: science of cities. Cambridge University Press, Cambridge, UK; 2014.
- Pickett STA, Cadenasso ML, Childers DL, Mcdonnell MJ, Zhou W. Evolution and future of urban ecological science: ecology in, of, and for the city. Ecosystem Health and Sustainability. 2016; 2: e01229. https://doi.org/10.1002/ehs2.1229
- Lepczyk CA, Warren PS, Machabée L, Kinzig AP, Mertig AG. Who feeds the birds? A comparison across regions. In: Lepczyk CA, Warren PS (eds) Urban bird ecology and conservation. University of California Press, Berkeley. 2012;pp 267–286. https://doi.org/10.1525/california/9780520273092.003. 0017
- Saberwal VK, Kothari A, Rangarajan M. People, parks, and wildlife: towards coexistence. Orient Longman, Delhi, India; 2001.
- Bagchi S, Mishra C. Living with large carnivores: predation on livestock by the snow leopard (Uncia uncia). Journal of Zoology. 2006; 268:217–224. https://doi.org/10.1111/j.1469-7998.2005.00030.x
- 46. Karanth KK, Naughton-Treves L, Defries R, Gopalaswamy AM. Living with Wildlife and Mitigating Conflicts Around Three Indian Protected Areas. Environmental Management. 2013; 52:1320–1332. <u>https://doi.org/10.1007/s00267-013-0162-1 PMID: 24026255</u>
- Knight RL, Grout DJ, Temple SA. Nest-defense behavior of the American Crow in urban and rural areas. Condor. 1987; 89:175–177.
- Kunca T, Yosef R. Differential nest-defense to perceived danger in urban and rural areas by female Eurasian sparrowhawk (*Accipiter nisus*). PeerJ. 2016; https://doi.org/10.7717/peerj.2070 PMID: 27441105
- 49. Moroni E, Crivelaro AZ, Soares TL, Gullermo-Ferreira R. Increased behavioural responses to human disturbance in breeding Burrowing Owls *Athene cunicularia*. Ibis.2017; 159: 854–859.
- Dingemanse NJ, Kazem AJ, Réale D, Wright J. Behavioural reaction norms: animal personality meets individual plasticity. Trends in Ecology & Evolution. 2010; 25:81–89. <u>https://doi.org/10.1016/j.tree.2009</u>. 07.013 PMID: 19748700
- Vincze E, Papp S, Preiszner B, Seress G, Bókony V, Liker A. Habituation to human disturbance is faster in urban than rural house sparrows. Behavioral Ecology. 2016; 27:1304–1313.
- 52. Newton I. Population ecology of raptors. Poyser, Berkhamstead, UK; 1979.
- 53. Knight RL, Temple SA. Why does intensity of avian nest defense increase during the nesting cycle? Auk. 1986; 103: 318–327.
- 54. Shea K, Roxburgh SH, Rauschert ES. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecology Letters. 2004; 7(6): 491–508. https://doi.org/10.1111/j. 1461-0248.2004.00600.x

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Received: 20 August 2018 Accepted: 27 December 2018 Published: xx xx xxxx

Human-attacks by an urban raptor are tied to human subsidies and religious practices

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Growing urbanization is increasing human-wildlife interactions, including attacks towards humans by vertebrate predators, an aspect that has received extremely scarce investigation. Here, we examined the ecological, landscape and human factors that may promote human-aggression by raptorial Black kites *Milvus migrans* in the 16-millions inhabitants megacity of Delhi (India). Physical attacks depended on human activities such as unhygienic waste management, ritual-feeding of kites (mainly operated by Muslims), human density, and presence of a balcony near the nest, suggesting an association between aggression and frequent-close exposure to humans and derived food-rewards. Surprisingly, while more than 100,000 people could be at risk of attack in any given moment, attitudes by local inhabitants were strikingly sympathetic towards the birds, even by injured persons, likely as a result of religious empathy. These results highlight the importance of socio-cultural factors for urban biota and how these may radically differentiate the under-studied cities of developing countries from those of western nations, thus broadening our picture of human-wildlife interactions in urban environments. The rapid sprawling of urban and suburban areas with their associated food-subsidies is likely to increase proximity and exposure of large predators to humans, and vice versa, leading to heightened worldwide conflicts.

There is growing interest in the interactions between human culture and animals, as evidenced by the rapid spread of studies in the field of ethnozoology¹⁻³. The need for integration of human socioeconomic and cultural variables into ecological research is particularly obvious in studies that focus directly on human-wildlife conflicts, or on expanding anthropogenic environments such as cities, where urban residents are confronted with a "novel" human-wildlife interface⁴⁻⁷.

In particular, worldwide urban residents are experiencing a growing frequency of encounters with wildlife due to increasing urbanization, human encroachment of natural habitats, expanding greenspaces within cities, intentional feeding to attract wildlife, and growing adaptation of animal species to urban ecosystems^{8–10}. While close encounters may be beneficial in reconnecting urban people with 'nature'^{11,12}, such increasing contacts are accompanied by an equally growing rate of human-wildlife conflicts, such as vehicle collisions, property damage, pet predation, disease transmission and even physical attacks on humans^{13–15}. Conflicts of this kind are typically difficult to manage because socio-political and cultural attitudes and perceptions often make mitigation controversial^{5,16}. This is especially pronounced in urban settings, which may pool together people with very different cultural backgrounds and with substantial differences in their interest or tolerance of wildlife, let alone of nuisance animals^{14,17,18}. Furthermore, urban animals may behave differently from their rural counterparts, thus requiring specially-designed mitigation measures¹⁹.

An extreme and sometimes dramatic form of human-wildlife conflict is represented by direct physical attacks on humans, which may cause psychological distress, diseases, injuries, sometimes severe or permanent ones, and even loss of life^{7,20–23}. Similarly to other forms of conflict, the frequency and severity of aggression on humans seem to be increasing in many urban areas^{24–27}. This creates an urgent need to know the potential drivers and risk

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Figure 1. A Black kite takes off from its nest on a pylon to attack the photographer, who is standing on a balcony (Photo credit: F. Sergio).

factors underpinning the attacks, in order to devise mitigation strategies and avoid conflict, which might prejudice peoples' perceptions of and actions towards wildlife in general²⁸⁻³⁰.

A special subset of these potentially-aggressive species is represented by vertebrate top predators, such as mammalian carnivores or birds of prey. Because of their armament, harm potential, and dangerous iconic nature in collective imagery, these species typically evoke more emotional responses and intolerance than other species³¹⁻³³, frequently leading to "hyper-perception of risk"⁵. For example, Kellert³⁴ showed that people tend to be more afraid of species that have the potential to harm them. Independently of perceptions, some of these predators have colonized many cities and increased dramatically in some urban areas in recent decades, sometimes reaching densities unparalleled in rural areas^{24,32,35-37}. In turn, this has increased encounters and conflict, sometimes with well demonstrated upturns in attack rates and even fatalities, frequently sensationalized by the public media²⁴⁻²⁷. In many cases, increased aggression has been linked with intentional and unintentional human feeding of the predators, resulting in consequent loss of fear³⁸⁻⁴⁰. Despite all the above, very few studies have examined the conditions that may predispose certain individuals to attack humans, and most of them have focused on mammals in rural areas^{7,41-43}. Thus, there is a great need for information from urban areas and other taxonomic groups to advance knowledge in this field. Here we assess the ecological, landscape and human factors that may promote aggression towards humans by raptorial Black Kites Milvus migrans (Fig. 1) in Delhi (India), a megacity of 16-million inhabitants, which hosts one of the largest concentrations of vertebrate predators of the world⁴⁴. In particular, we tested the hypothesis that individuals more exposed to human feeding and subsidies may be more likely to attack humans.

The Black Kite (hereafter "kite") is a medium-sized, opportunistic predator and facultative scavenger. It is considered the most successful raptor in the world, due to its capability to withstand anthropogenic habitat change and even breed in high numbers alongside dense human populations within cities, especially in tropical areas⁴⁵. Throughout its distribution, there are reports of individuals snatching food from humans, sometimes in aggressive ways, up to the point of being considered a local nuisance^{46,47}. In India, the native, resident subspecies *M. m.* govinda is synurbic⁴⁸, i.e. it occurs almost exclusively in close association with humans in towns and cities⁴⁹. In Delhi, where this study was conducted, kites breed throughout the city, often a few meters from human habitation, and locally reach extremely high densities, thanks to the exploitation of human food subsidies facilitated by inefficient refuse disposal and by religious kite-feeding practices^{44,50}. These centuries-old religious offerings (hereafter termed 'ritualized-feeding') consist in throwing meat scraps into the air for the kites to catch and are made for a variety of reasons, such as asking for blessings and relief from sins and worries^{51,52}. Whilst meat-offering is practiced by a number of communities, in Delhi it is especially prevalent amongst members of Islamic faith, whose numbers are concentrated in well-defined portions of the city (hereafter 'Muslim colonies') where large quantities of meat are tossed to kites at predictable hours each day, sometimes causing hundreds of kites to congregate. Breeding individuals of this kite population often dive-bomb, scratch and harm humans with their talons when these approach their nest, sometimes causing deep cuts (Fig. 1). At times, these injuries may require medical examination because of the potential of subsequent infections, given kites' frequent foraging on rotting organic waste.

Results

To investigate the determinants of kites' attacks on humans, we recorded aggressive events during routine visits to kites breeding sites, in which nests were approached and examined by a team of three people in a standardized manner (see Methods). Kites were classified as attacking when they dive-bombed and made physical contact with any member of the research team. In the four years of research, the percentage of attacking pairs averaged 25.5%

Explanatory variables in each model ^a	Degrees of freedom	AICc	Delta AICc	Model weight
Hygiene score + Breeding success	5	66.29	0.00	0.34
Balcony + Hygiene score + Breeding success + Access to Muslim colonies + Balcony * Access to Muslim colonies	8	67.77	1.48	0.16
Hygiene score + Breeding success + Access to Muslim colonies	6	68.08	1.79	0.14
Balcony + Hygiene score + Breeding success	6	68.18	1.89	0.13
Hygiene score + Urban cover + Breeding success	6	68.41	2.12	0.12
Human density + Hygiene score + Breeding success	6	68.48	2.19	0.11

Table 1. Top ranking (i.e. with $\Delta AICc < 3$) generalised linear mixed models with binomial errors and a logit link function testing the effect of environmental, urban and human variables on likelihood of aggressive attack against humans (attacking vs control pair) by a nesting kite pair (N = 204 trials from 72 independent territories). Territory-identity nested within plot-identity was fitted as a random effect to all models. See Supplementary Table S.1 for the description of explanatory variables. ^aVariables presented to the model: Number of people, Balcony, Urban cover, Green cover, Hygiene score, Human density, Access to Muslim colonies, Access to Muslim colonies * Hygiene score, Access to Muslim colonies * Urban cover, Access to Muslim colonies * Balcony.

Variable	B±SE	Z test	P value
Breeding Success	28.69 ± 7.33	3.91	< 0.0001
Hygiene score	30.4 ± 7.9	3.86	0.0001
Access to Muslim subsidies	1.31 ± 4.1	0.32	0.75
Balcony	8.57 ± 7.77	1.1	0.27
Balcony * Access to Muslim colonies	17.19 ± 6.86	2.54	0.012
Human density	1.14 ± 0.19	5.94	< 0.0001
Urban Cover	0.57 ± 7.46	0.08	0.94
Intercept	-76.2 ± 21.37	3.56	0.0003

Table 2. Model averaged coefficients for the explanatory variables that entered the top-ranking models of Table 1.

(range 18.0–37.7%), and attacking individuals were present at 36 (i.e. 31.9%) of 113 separate territories checked at least once for reproduction. Twenty-one of these 36 attacking pairs but none of the 36 non-attacking pairs had a history of past local attacks, as from interviews with local inhabitants (χ^2 =15.09, P < 0.0001), suggesting that pairs identified as aggressive by our trials were not responding to an unusual stimulus, but were already known to be problematic pairs well before our research activities. In all attacks during our trials, kites dive-bombed at high speed and tried to hit the target-person on the head, typically with the open hallux and closed phalanges, so as to either scratch or knock the target-person on the head. Due to escape movements, scratches were sometimes re-directed on the forehead or on the neck or shoulders. All attacks were from behind and never when a person was staring at a kite dive-bombing towards the group.

To investigate the potential drivers of aggression, we built a logistic mixed model discriminating between attacking and non-attacking kites on the basis of a series of ecological, landscape and human socio-religious variables (see Methods). In this model, the likelihood of attack increased with kite breeding success, with more human waste around the nest (higher hygiene score), with higher access to Muslim subsidies, with higher human density in the streets and with the presence of a close-by balcony facing the nest (Tables 1 and 2, Fig. 2). The interaction between balcony presence and access to Muslim subsidies was also important: kite aggression was more likely for pairs that had both a balcony close by and high access to Muslim subsidies (Fig. 3).

Discussion

Our results contribute to advance and integrate different fields of research such as ethnozoology, urban ecology and the resolution of human-wildlife conflicts. Below, we (1) explain the mechanisms that may generate the observed patterns and (2) discuss the importance of our findings for each of the above three disciplines.

Kite attacks on humans were not randomly distributed through the city and responded to a series of indicators of human activities, such as unhygienic management of waste disposal, Muslim ritual-feeding, and the intensity of human activity in the streets. This configuration of socio-religious features is preferred by the kites of Delhi because of its high food availability in the form of ritual subsidies and organic garbage⁵⁰ and may have promoted aggression in three non-exclusive ways. First, kites feeding on ritual subsidies or organic waste (frequently accomplished side by side with indigent people digging for useful materials) are frequently in close proximity to people, which may have lowered their fear of humans. Second, close proximity was frequently rewarded with food, which may have reinforced such loss of fear. Third, aggression varied with the interaction between access to Muslim ritual-subsidies and the presence of a balcony in the immediate proximity of the nest (Fig. 3). Thus, Muslim subsidies increased aggression-likelihood more markedly for pairs that nested in the immediate proximity of a balcony and, conversely, the presence of a balcony heightened aggression for pairs with ready access to Muslim



Figure 2. The likelihood of attacking humans by a breeding Black kite pair increased with: its breeding success (panel a, left bars), with more human waste around its nest (higher hygiene score, panel a, central bars), with the presence of a balcony in close proximity of the pair's breeding site (panel a, right bars), with higher access to ritual subsidies from Muslim colonies (panel b), and with higher human density in the streets of the nest surroundings (panel c). Error bars represent 1 SE.



Figure 3. Likelihood of aggressive attack on humans by nesting Black kites in relation to access to ritual-feeding sites (Muslim colonies) and the presence of a balcony within 20 m radius of the nest. Error bars represent 1 SE.

subsidies. This suggests that peak aggression was promoted by the synergy of these two exposures to frequent and close encounters with humans.

In addition, human attacks were linked to successful reproduction. This could be promoted by two non-exclusive mechanisms: (1) parents could have a sense of the quality of their parental investment (e.g. based on their own or their offspring body condition) and defend more fiercely when success-prospects are high, as shown in other species⁵³⁻⁵⁵; and (2) aggressive behaviour towards humans paralleled the capability to repel other more common nest predators, such as crows or monkeys⁴⁴, leading to a lower probability of nest failure from predation. Independently of motivational or causational mechanisms, if human-attacking pairs are more productive, there is a possibility that such behaviour could become more frequent in the population in the future, particularly so if aggression propensity were genetically inherited or culturally transmitted (e.g. by young kites emulating their parents' defense tactics once adult).

Implications for urban ecology. Implications for urban ecology were clear and profound. First, kite aggression did not respond to landscape composition or other classical ecological variables, but rather to a series of socio-religious and cultural features. This represents a clear-cut example of the importance of integrating human cultural factors into research programs in urban ecology. While human presence and action is one of the most defining characteristics of urban ecosystems⁴, few studies on urban animals explicitly incorporate human culture and perceptions into their design^{56,57}. When such aspects are tested, they are usually found to be key factors for urban ecology and conservation. For example, human socio-economic status has been shown to affect avian diversity, occurrence and distribution^{58–60}, while human perceptions of affinity/aversion towards certain animals varied across an urban-rural gradient, with important repercussions for potential conservation action⁶¹.

Second, some studies have shown that bolder, more aggressive individuals are more likely to colonize urban environments^{62–65}. These links have usually been shown in comparisons of urban vs rural populations. If we consider the propensity to attack humans observed in this study as a measure of boldness, then our data extend this urban-rural comparison to individual variation within a city. Under this scenario, boldness in human tolerance may continue to be a key modulator of urban adaptation and exploitation even long after the initial colonization of the urban environment.

Third, the occurrence of the attacks in a highly-subsidized and thus high-density animal population coexisting with a dense human population generated a problem of unusual magnitude. First of all, only 25-30% of kite pairs attacked humans, which compares with 19 and 73% of Australian magpies Gymnorhina tibicen and Masked lapwings Vanellus miles, two species also renowned for their attacks on humans in urban settings^{20,66}. However, even if only one in three or four pairs attacked humans, the local high density of kites over a very large area (average of 15 pairs/km²)⁴⁴ implies that Delhi could easily hold over 5600 aggressive pairs. If we further consider that human density is high in Delhi and that attacking pairs were disproportionately concentrated in areas of higher human density, several thousand people could be potentially exposed to kites' attacks every year. For example, during our tests of approximately 20 min duration, there were on average 18 people in the immediate proximity of the nest of an attacking pair. If this figure is representative, then multiplying it by 5600 aggressive pairs would imply that more than 101,000 people could be passing/standing within attacking-radius of an aggressive kite pair basically in every given moment of the day. Furthermore, most of the pairs that attacked us had a clear history of past attacks on local inhabitants, implying that our type of deliberate nest intrusion did not somehow exaggerate the extreme attacks that we recorded. Attacking individuals were 'problematic' already well before our activities. Conflicts of this magnitude and concentration would be unlikely in any rural setting and underline how urban ecosystems may pose novel challenges and require new approaches to wildlife management and conservation¹⁹.

Implications for research on human-wildlife conflict. This study confirmed and extended current knowledge on the drivers of human-attacks by vertebrate animals. First, habituation to human proximity and animal feeding have been frequently reported as drivers of aggression on humans by mammalian carnivores and primates^{38–40,42,67}. Our findings support these views, extend them to avian predators and thus suggest that they may represent generalized drivers of potential aggression across distantly related taxa. Second, human conflict with predators has often been associated with food scarcity driving low-quality, food-deprived individuals in close contact with humans^{7,66,68–71}. In our case, attacks were concentrated in optimal, preferred habitat, and perpetrated by more productive, likely higher-quality individuals. Such dynamics may be more typical of synanthropic urban predators, whose high-quality individuals may be drawn to an abundant food supply but get habituated to humans in the process of accessing it. While food availability in both cases may mediate aggression, its enactment by individuals of different quality and breeding-potential may have strong repercussions for future trends in aggression rates, with obvious forecasting and management implications. This confirms the importance of resource-distribution in wildlife-human conflicts^{10,72} and further remarks how the management of synanthropic or urban wildlife may require specially-designed techniques¹⁹.

Finally, social factors and cultural perceptions have been identified as important drivers of the intensity of human-wildlife conflict, but are seldom taken into consideration^{5,7,42,61,73,74}. Our results not only stressed the importance of socio-religious variables as key drivers of the conflict, but also show how they can enter the equally key human-part of conflict resolution. In fact, despite the above-reported magnitude of the problem, interviews with 140 persons encountered under the nests of attacking pairs uncovered extremely positive attitudes of local inhabitants towards the birds, even by individuals who were previously injured (authors' unpubl. data). Overall, most people expressed fear for the attacks, as logically expected, but 100% of the respondents justified and showed explicit sympathy for the kites. Sympathy was motivated in two ways: (1) kites were protecting their offspring (i.e. doing their duty of good parents), and (2) humans have destroyed and degraded natural habitats and wildlife has no option but to live with humans, implying the ultimate fault was of people rather than kites. In turn, local communities, all of them of either the Islamic or the Hindu faith, tied such empathy to religious views about kites

and about wildlife in general. Muslims mainly revered kites as sort of sacred, given their role of "winged emissaries" that metaphorically take away towards the sky their sins, worries, or prayers, symbolized by the meat offered during ritual-feedings^{51,52}. Hindus believe that a soul undergoes body transformations, that all life forms are thus connected to one ultimate god form and thus they respected kites as part of their wider tolerance to all wildlife species as god's beings. Finally, positive attitudes were probably further promoted by the fact that (1) attacks only occurred during a minor, predictable part of the year (duration of about two months), (2) that most injuries were generally light due to local people learning to avoid certain sites, and (3) that people were usually well aware of the useful ecosystem service provided to their neighbourhood by kites, which in Delhi remove more than 3900 tons of organic waste per year (authors' unpubl. data).

Whatever the underlying motivation, these positive attitudes clearly translated into actions. All people reported taking (non-harmful) action to avoid confrontations, which may further reinforce kite aggression through additional reward. This included avoiding the nest proximity, dissuading children from using the parks or certain sections of the park, or refraining from using the balcony until the nestlings fledged. Some schools and canteens have changed their rules to make children and customers eat their lunch inside the premises rather than outdoor close to an attacking pair. In one case, the husband of a woman who received a serious scratch on her face enclosed the balcony with a volleyball net in order to get protection while continuing to use the balcony. In all these cases, no attempts at retaliatory measures, such as nest removal or killing the birds, were ever noticed or reported. On few occasions, local inhabitants enquired the possibility that we could remove the nest, but strongly specifying that it would have to be done after the nestlings had fledged. They also asked information about whether there could be non-harmful ways to dissuade kites from nesting at specific locations and about how to behave so as to avoid being attacked. Note that such extreme tolerance, even after injury, would be extremely unlikely by denizens of the western world, where conflicts of similar kind often end up in court after retaliatory nest removals or illegal killings^{7,75} and where urban people are often reported as disconnected from nature and profoundly puzzled by conflicts with wildlife, frequently seen as a nuisance to remove^{10,18,76,77}. Finally, to date the few studies that have examined the role of human religion, ethnicity, or social factors in human-wildlife conflict have shown how they can shape human attitudes and perceptions and thus intervene on the human side of the conflict^{5,7,42,61,73,74}. In our case, we show that they can also affect the animal side of the conflict-interaction by shaping animal aggression through reward and habituation, thus confirming and extending their importance.

Implications for ethnozoology and the importance of human cultural factors. Human socio-cultural factors permeated all results and allowed more realistic insights into the drivers of a human-wildlife conflict. In particular, kite attacks on humans responded to a geography of human religion, hygiene and poverty, and were concentrated within the productive sector of the kite population located at the high-end of the human-exploitation axis. Notably, kite behaviour was keenly adjusted to humans, tolerating them at close range when feeding but attacking them when provoked, while humans equally responded to kite behaviour, encouraging their ecosystem service function and avoiding them without retaliation when attacked. In this sense, kites and humans could be contextualized as participants in a "coupled-system" where each of the two actors co-shaped each other's socio-ecological space through repeated interactions, a phenomenon already suggested for other species⁷⁸⁻⁸¹. Human culture was thus key to identifying drivers of attacks and problematic sectors of the city. It also intervened to alleviate the conflict, as current evidence suggested that, at present, the aesthetic, cultural, spiritual and ecosystem-service benefits offered by kites clearly outweighed the local, albeit diffuse discomfort provided by aggressive individuals. This highlights a growing appreciation of the value of intangible benefits provided by wildlife to humans^{12,74,82,83}, but most of all, it shows how ethnozoological approaches can improve ecological insight and bridge the gap between different disciplines such as behavioural ecology, wildlife management and urban ecology through direct incorporation of human socio-cultural aspects^{2,3}. In fact, human-wildlife conflicts have been identified as prime examples of research and management activities where incorporation of socio-cultural tools is direly needed^{3,4}. In conclusion, given that many predatory vertebrates are likely to be attracted by subsidies from a growing human population worldwide⁸⁴, conflicts promoted by close exposure to humans, as portrayed here, are likely to increase.

Methods

Ethics statement. This research is part of a larger and long-term study on the demography of Black Kites in Delhi. We received the permits to conduct the fieldwork from the office of the Additional Principal Chief Conservator of Forests (APCCF), the Government of National Capital Territory of Delhi under the provisions of the Wildlife Protection Act, 1972 (permit number: CF/LC/105/07/HQ/10504-8). The Training, Research, and Academic Council (TRAC) of the Wildlife Institute of India, Dehradun (WII), gave bioethical approval for the research protocols. We performed all methods in accordance with the relevant guidelines and regulations laid out by TRAC WII with respect to study animal and human participants. We also sought informed consent from all the participants (or their legal guardians) for the semi-structured interviews (see below). We took all precautions to ensure researcher and animal safety, and maintained anonymity of the human respondents at all the stages of data recording during the field trials. All members of the field team were regularly administered with preventive vaccination, they wore thick hats/helmets and appropriate protective clothing so as to ensure safety.

Study Area. Delhi is a megacity of more than 16 million inhabitants, covering an area of 1500 km² and in constant expansion⁸⁵. Three aspects of Delhi are important for kites. First, much of the city is characterized by poor solid waste management, which affords plenty of food to kites in the form of carrion or refuse. Second, many people engage in the centuries-old religious practice of feeding meat scraps to kites (hereafter termed 'ritualized-feeding'), typically offered by throwing meat into the air for the birds to catch. These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries^{51,52}. Whilst meat-offering is practiced by a number of communities, in Delhi it is especially prevalent amongst members of Islamic faith,

whose numbers are concentrated in well-defined portions of the city (hereafter 'Muslim colonies') where large quantities of meat are tossed to kites at predictable hours each day, sometimes causing hundreds of kites to congregate. Third, Delhi retains reasonable green cover, thus providing abundant nesting habitat for kites⁸⁶.

Fieldwork procedures and statistical analysis. Data on attacks were collected during nest-checks in 2013-2016, conducted at 20 plots randomly scattered throughout the city in order to cover all its possible urban settings, from semi-natural to extremely built-up sites (see^{44,50} for details of plots and nest checks). On each occasion, nests were visited in a standardised manner: a team of three people approached the nest directly from a point approximately 50 m from the nest, chosen to be clearly visible to a kite perched in the nest area. One person (always the same one) then proceeded to climb the nest. A kite pair was classified as attacking when either of the two parents dive-bombed and made physical contact with any member of the team. To examine the characteristics that may affect the likelihood of aggression, we compared attacking and non-attacking pairs in the following manner. First, for each pair that attacked us, we chose a non-attacking pair that: (1) had eggs or chicks of similar age, (2) that was checked in the same year and on the same or preceding-following day, (3) that had received a similar number of previous visits by our team, and (4) that had a similar tree-arrangement configuration (nest in an isolated tree, line of trees, parkland or continuous woodland). This allowed us to investigate aggression while removing the potentially confounding effects of year, date, breeding stage, previous visit and local habitat-structure. Second, for all attacking and non-attacking pairs we collected a number of landscape and human variables (Supplementary Table S.1), based on our knowledge of kite ecology and of a previous study on habitat preferences by Delhi kites⁵⁰. These variables estimated the structure and composition of the urban landscape around the nests, their local availability of organic garbage, their access to Muslim ritual-subsidies, the local density of humans around the nest and in the surrounding streets, and the close exposure to human presence through the presence-absence of an open balcony within 20 m of the nest (details in Supplementary Table S.1). Thus, they characterized each pair on the basis of its surrounding urban characteristics, food availability, and exposure to humans as well as their subsidies. Third, we used a logistic mixed model⁸⁷, with pair-identity nested within plot-identity, to discriminate between attacking and non-attacking pairs on the basis of the landscape and human variables. To reduce collinearity and the number of variables presented to multivariate models, we employed the method of variable reduction proposed by Green⁸⁸. In this method, pairs of strongly intercorrelated variables (r > 0.6) are considered as estimates of a single underlying factor. Only one of the two is retained for analysis, usually the one likely to be perceived as more important by the study organism. Of the remaining variables, only those for which significant univariate differences (P < 0.1) were detected between attacking and non-attacking pairs were included in the logistic model (Supplementary Table A.2). Univariate differences were carried out by means of t-tests and χ^2 tests. Model building was implemented through an information-theoretic approach, following recommendations by⁸⁹⁻⁹¹. We used the "dredge" function of the MuMIn package to rank competing models on the basis of their weight and $AICc^{89}$. Models within 3 AICc units of the top model were selected for model averaging, implemented through the MuMIn package. All the analyses were performed through R 3.4.3⁹².

Finally, to gain an understanding of the extent and impact of attacks on local communities, we approached and interviewed all the people we encountered during our trials in the immediate proximity of the nests of attacking and non-attacking pairs (N = 278 interviews). This allowed us to test whether pairs that attacked us also had a higher probability of previously attacking local people, i.e. before and independently of our activities. Detailed analysis of the interviews will be reported elsewhere, but in the Discussion, we delineate the main local opinions qualitatively, in order to place the conflict in the context of local attitudes. Throughout, all tests are two-tailed, statistical significance was set at \leq 0.05 and means are given with 1 SE. The dataset of the current study is available on reasonable request from the corresponding author.

Data Availability

Given that a part of the data is funded by a Foundation who has shared possession of the generated datasets, the data for the manuscript are available upon reasonable request from the authors.

References

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- 1. Tidemann, S. & Gosler, A.G. Ethno-ornithology: birds, indigenous people, culture and society. (Earthscan, 2010).
- Alves, R. R. N. Relationships between fauna and people and the role of ethnozoology in animal conservation. *Ethnobiol. Conserv.* 1, 1–69 (2012).
- 3. Alves, R. R. N. & Albuquerque, U. P. Ethnozoology: animals in our lives. (Elsevier, 2018).
- 4. Alberti M. Advances in urban ecology: integrating humans and ecological processes in urban ecosystems. (Springer, 2008).
- Dickman, A. J. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. Anim. Conserv. 13, 458–466 (2010).
- 6. Redpath, S. M. et al. Understanding and Managing conservation conflicts. Trends Ecol. Evol. 28, 100-109 (2013).
- 7. Torres, D. F., Oliveira, E. S. & Alves, R. R. N. Conflicts between humans and terrestrial vertebrates: a global review. *Trop. Conserv. Sci.* 11, 1–15 (2018a).
- Marzluff, J. et al. (Eds). Urban ecology: an international perspective on the interaction between humans and nature. (Springer, 2008).
 Gaston, K. J. Urban ecology. (Cambridge University Press, 2010).
- Soulsbury, C. D. & White, P. C. L. Human-wildlife interactions in urban areas: a review of conflicts, benefits and opportunities. Wildl. Res. 42, 541–553 (2015).
- Hosey, G. & Melfi, V. Human-animal interactions, relationships and bonds: a review and analysis of the literature. *Int. J. Comp. Psychol.* 27, 117–142 (2014).
- Cox, D. T. C. & Gaston, K. J. Urban bird feeding: connecting people with nature. PLoS ONE 11(7), e0158717, https://doi.org/10.1371/ journal.pone.0158717 (2016).
- 13. Conover, M. R. Resolving human-wildlife conflicts: the science of wildlife damage management. (CRC Press, 2002).
- 14. Hadidian, J. Wildlife in U.S. cities: managing unwanted animals. Animals 5, 1092-1113 (2015).
- 15. Adams, C. E. Urban wildlife management. (CRC Press, 2013).
- 16. Messmer, T. A. The emergence of human-wildlife conflict management: turning challenges to opportunities. *Int. Biodeterior. Biodegradation* **45**, 97–102 (2000).
- Conover, M. R. Wildlife management by metropolitan residents in the United States: practices, perceptions, costs, and values. Wildl. Soc. Bull. 25, 306–311 (1997).
- Bjerke, T. & Østdahl, T. Animal-related attitudes and activities in an urban population. Anthrozoös 17, Iss. 2, https://doi. org/10.2752/089279304786991783 (2004).
- 19. Ditchkoff, S. S., Saafeld, S. T. & Gibson, C. J. Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosyst.* 9, 5–12 (2006).
- Jones, D. & Thomas, L. Attacks on humans by Australian magpies: management of an extreme suburban human-wildlife conflict. Wildl. Soc. Bull. 27, 473–478 (1999).
- Kofron, C. P. Attacks to humans and domestic animals by the southern cassowary (Casuarius casuarius johnsonii) in Queensland, Australia. J. Zool. 249, 375–381 (1999).
- Kushnir, H., Leitner, H., Ikanda, D. & Packer, C. Human and ecological risk factors for unprovoked lion attacks on humans in southeastern Tanzania. *Human Dim. Wildl.* 15, 315–331 (2010).
- 23. Sundarshan, M. K. *et al.* Assessing the burden of human rabies in India: results of a national multi-center epidemiological survey. *Int. J. Infect. Dis.* **11**, 29–35 (2017).
- Timm, R. M., Baker, R. O., Bennett, J. R. & Coolahan, C. C. Coyote attacks: an increasing suburban problem. Trans. North Am. Wildl. Nat. Res. Conf. 69, 67–88 (2004).
- Siemer, W. F., Hart, S., Decker, D. J. & Shanahan, J. E. Factors that influence concern about human-black bear interactions in residential settings. *Human Dim. Wildl.* 14, 185–197 (2009).
- 26. Thornton, C. & Quinn, M. S. Coexisting with cougars: public perceptions, attitudes, and awareness of cougars on the urban-rural fringe of Calgary, Alberta, Canada. *Human-Wildlife Conflicts* **3**, 282–295 (2009).
- Bhatia, S., Athreya, V., Grenyer, R. & MacDonald, D. W. Understanding the role of representations of human-leopard conflict in Mumbai through media-content analysis. *Conserv. Biol.* 27, 588–594 (2013).
- 28. St John, F. A. V. *et al.* Identifying indicators of illegal behaviour: carnivore killing in human-managed landscapes. *Proc. R. Soc. B.* **279**, 804–812 (2011).
- Dickman, A. J., Hazzah, L., Carbone, C. & Durant, S. M. Carnivores, culture and 'contagious' conflict; multiple factors influence perceived problems with carnivores in Tanzania's Ruaha landscape. *Biol. Conserv.* 178, 19.27 (2014).
- 30. Hazzah, L., Bath, A., Dolrenry, S., Dickman, A. & Frank, L. From attitudes to actions: predictors of lion killing by Maasai warriors. *PLoS ONE* **12**(1), e0170796 (2017).
- 31. Fascione, N., Delach, A. & Smith, M. E. People and predators: from conflict to coexistence. (Island Press, 2004).
- 32. Gehrt, S. D., Riley, S. P. D. & Cypher, B. L. Urban carnivores: ecology, conflict and conservation. (The Johns Hopkins University Press, 2010).
- Elliot, E. E., Vallance, S. & Molles, L. E. Coexisting with coyotes (*Canis latrans*) in an urban environment. Urban Ecosyst. 19, 1335–1350 (2016).
- 34. Kellert, S. R. American attitudes toward and knowledge of animals: an update. International. *Journal for the Study of Animal problems* 1, 87-119 (1980).
- 35. Bird, D., Varland, D. & Negro, J. J. Raptors in human landscapes. (Academic Press, 1996).
- 36. Rutz, C. The establishment of an urban bird population. J. Anim. Ecol. 77, 1008–1019 (2008).
- 37. Bateman, P. W. & Fleming, P. A. Big city life: carnivores in urban environments. J. Zool. 287, 1-23 (2012).
- 38. McCullough, D. R. Behavior, bears, and humans. Wildl. Soc. Bull. 10, 27-33 (1982).
- Bounds, D. L. & Shaw, W. W. Managing coyotes in U.S. national parks: human-coyote interactions. Natural Areas Journal 14, 280–284 (1994).
- Thompson, J., Shirreffs, I. & McPhail, I. Dingoes on Fraser Island: tourism dream or management nightmare. *Human Dim. Wildl.* 8, 37–47 (2003).
- Nyhus, P. J. & Tilson, R. Characterizing human-tiger conflict in Sumatra, Indonesia: implications for conservation. Oryx 38, 68–74 (2004).
- Hockings, K. J., Yamakochi, G., Kabasawa, A. & Matsuzawa, T. Attacks on local persons by chimpanzees in Bossou, Republic of Guinea: long-term perspectives. Am. J. Primatol. 72, 887–896 (2010).
- 43. Kushnir, H. *et al.* Using landscape characteristics to predict lion attacks on humans in south-eastern Tanzania. *Afr. J. Ecol.* **52**, 524–532 (2014).
- 44. Kumar, N., Mohan, D., Jhala, Y. V., Qureshi, Q. & Sergio, F. Density, laying date, breeding success and diet of Black Kites Milvus migrans govinda in the city of Delhi (India). Bird Study 61, 1–8 (2014).
- 45. Ferguson-Lees, J. & Christie, D. A. Raptors of the world. (Houghton Miffin Company, 2001).
- 46. Parker, J. W. Raptor attacks on people. J. Raptor Res. 33, 63-66 (1999).
- 47. Galbreath, D. M., Ichinose, T., Furutani, T., Yan, W. & Higuchi, H. Urbanization and its implication for avian aggression: a case study of urban black kites (*Milvus migrans*) along Sagami Bay in japan. *Landscape Ecol.* **29**, 169–178 (2014).
- 48. Francis, R. A. & Chadwick, M. A. What makes a species synurbic? Applied Geography 32, 514-521 (2012).
- 49. Naoroji, R. Birds of prey of the Indian subcontinent. (Christopher Helm/A&C Black Publishers Ltd., 2006)
- 50. Kumar, N. *et al.* Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools. *Urban Ecosyst.* **21**, 339–349 (2018).
- Pinault, D. Raw meat skyward: Pariah-kite rituals in Lahore in Comparative Islamic studies: notes from the fortune-telling parrot: Islam and the struggle for religious pluralism in Pakistan (ed. Pinault, D.), 108–121 (Equinox Publishing Ltd, 2008).
- Taneja, A. V. Saintly animals: the shifting moral and ecological landscapes of North India. Comparative Studies of South Asia, Africa and the Middle East 35, 204–221 (2015).
- 53. Montgomerie, R. D. & Weatherhead, P. K. Risks and rewards of nest defence by parent birds. Quarter. Rev. Biol. 63, 167-187 (1988).
- Redondo, T. Avian nest defence: theoretical models and evidence. *Behaviour* 111, 161–195 (1989).
 Sergio, F. & Bogliani, G. Nest defense as parental care in the Northern Hobby. *Auk* 118, 1047–1052 (2001).
- Grimm, N. B., Steward, J. M. G., Pickett, T. A. & Redman, C. L. Integrated approaches to long-term studies of urban ecosystems. BioScience 50, 571–584 (2000).
- 57. Liu, J. et al. Complexity of coupled human and natural systems. Nature 31, 1513–1516.
- Shaw, L. M., Chamberlain, D. & Evans, M. The House Sparrow Passer domesticus in urban areas: reviewing a possible link between post-decline distribution and human socioeconomic status. J. Ornithol. 149, 293–299 (2008).
- Van Heezig, Y. & Hight, S. R. Socio-economic-driven differences in bird-feeding practices exacerbate existing inequities in opportunities to see native birds in cities. J. Urban Ecol. https://doi.org/10.1093/jue/jux011 (2017).
- Van Heezig, Y., Freeman, C., Porter, S. & Dickinson, K. J. M. Garden size, householder knowledge, and socio-economic status influence plant and bird diversity at the scale of individual gardens. *Ecosystems* 16, 1442–1454 (2013).
- de Oliveira, J. V., de F Lopes, S., Barboza, R. R. D. & Alves, R. R. N. To preserve, or not to preserve, that is the question: urban and rural student attitudes towards wild vertebrates. *Environ. Dev. Sustain.*, https://doi.org/10.1007/s10668-018-0083-5 (2018).
- 62. Møller, A. P. Flight distance of urban birds, predation, and selection for urban life. Behav. Ecol and Socio. 63(1), 63-75 (2008).

- 63. Evans, J. E., Boudreau, K. & Hyman, J. Behavioural syndromes in urban and rural populations of song sparrows. *Ethology* **116**, 588–595 (2010).
- 64. Carrete, M. & Tella, J. L. Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PLoS One* **6**(4), e18859 (2011).
- 65. Lowry, H. & Wong, B. B. M. Behavioural responses of wildlife to urban environments. Biol. Rev. 88, 537-549 (2012).
- 66. Lewis, D. L. *et al.* Foraging ecology of black bears in urban environments: guidance for human-bear conflict mitigation. *Ecosphere* **6**, 1–18 (2015).
- 67. Fa, J. E. Visitor-directed aggression among the Gibraltar macaques. Zoo Biol. 11, 43-52 (1992).
- Patterson, B., Kasiki, S. M., Selempo, E. & Kays, R. W. Livestock predation by lions (Panthera leo) and other carnivores on ranches neighboring Tsavo National Park, Kenya. Biol. Conserv. 119, 507–516 (2004).
- Graham, K., Beckerman, A. P. & Thirgood, S. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biol. Conserv.* 122, 159-71 (2005).
- 70. Murray, M. H. & St. Clair, C. C. Predictable features attract urban coyotes to residential yards. J. Wildl. Manage. 81, 593–600 (2017). 71. Torres et al. 2018b
- Blackwell, B. F. *et al.* No single solution: application of behavioural principles in mitigating human-wildlife conflict. *Anim. Behav.* 120, 245–254 (2016).
- Hazzah, L., Mulder, B. M. & Frank, L. Lions and warriors: social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. *Biol. Conserv.* 142, 2428–2437 (2009).
- 74. Kansky, R. & Knight, A. T. Key factors driving attitudes towards large mammals in conflict with humans. *Biol. Conserv.* 17, 93–105 (2014).
- 75. Lees, D. *et al.* Swooping in the suburbs: parental defence of an abundant aggressive urban bird against humans. *Animals* **3**, 754–766 (2013).
- 76. Sterba, J. Nature wars: the incredible story of how wildlife comebacks turned backyards into battlegrounds. (Crown Publishers, 2012).
- 77. Miller, J. R. Biodiversity conservation and the extinction of experience. Trends Ecol. Evol. 20, 430-434 (2005).
- 78. Marzluff, J. M. & Angell, T. Cultural coevolution: how the human bond with crows and ravens extends theory and raises new questions. *J. Ecol. Anthropol.* **9**, 69–75 (2005).
- Clucas, B. & Marzluff, J. M. Coupled relationships between humans and other organisms in urban areas In: Urban ecology: patterns, processes, and applications (ed. Niemelä, J.), 135–147 (Oxford University Press, 2011).
- Riley, E. P. & Priston, N. E. C. Macaques in farms and folklore: exploring the human-nonhuman primate interface in Sulawesi, Indonesia. Am. J. Primatol. 71, 825–839 (2010).
- 81. Fuentes, A. Ethnoprimatology and the anthropology of the human-primate interface. Annu. Rev. Anthrop. 41, 101–117 (2012).
- Maller, C., Townsend, M., Prior, A., Brown, P. & St. Leger, L. Healthy nature healthy people: contact with nature' as an upstream health promotion intervention for populations. *Health Promotion International* 21, 45–54 (2006).
- Keniger, L. E., Gaston, K. J., Irvine, K. N. & Fuller, R. A. What are the Benefits of Interacting withNature? *Journal of Environmental Research and Public Health* 10, 913–935 (2013).
- 84. Newsome, T. M. et al. The ecological effects of providing resource subsidies to predators. Global Ecol. Biogeog. 24, 1-11 (2015).
- Census Organisation of India. Office of the Registrar General & Census Commissioner, India, http://censusindia.gov.in/2011census (2011).
- Paul, S. & Nagendra, H. Vegetation change and fragmentation in the mega city of Delhi: mapping 25 years of change. Appl Geogr. 58, 153–166 (2015).
- Zuur, A. F. Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. Mixed effects models and extensions in ecology with R. (Springer, 2009).
- 88. Green, R. H. Sampling design and statistical methods for environmental biologists. (John Wiley & Sons, 1979).
- Grueber, C. E., Nakagawa, S., Laws, R. J. & Jamieson, I. G. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699–711 (2011).
- Richards, S. A., Whittingham, M. J. & Stephans, P. A. Model selection and model averaging in behavioural ecology: the utility of IT-AIC framework. *Behav. Ecol. Sociobiol.* 65, 77–89 (2011).
- 91. Galipaud, M., Gillingham, M. A. F., David, M. & Dechaume-Moncharmont, F. Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. *Methods Ecol. Evol.* 5, 983–991 (2014).
- 92. R Development Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna (2017).

Acknowledgements

We thank Dr. R. Dor and two anonymous reviewers for constructive comments that greatly improved the manuscript, and Ujjwal Kumar and the Director, Dean and Research Coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Delhi Transport Corporation, Civic bodies of the Government of NCT of Delhi helped with legal permits, and the Director of the National Zoological Park of New Delhi gave access to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We thank Laxmi Narayan, Prince Kumar, Poonam and all the members of the "Black Kite Project Group" for help in the field, especially U. Gupta, H. Malhotra, A. Singh, P. Kumar, H. Singh, U. Nair and M. Singh. The project was funded by the Raptor Research and Conservation Foundation (Mumbai) and by the Govt. of India, Ministry of Environment, Forest and Climate Change. NK was funded by the Felix Scholarship Trust and Somerville College, Oxford University and FS by project CGL2015- 69445-P of the Spanish Ministry of Economy and Competitiveness with Feder Funds.

Author Contributions

N.K., Y.V.J., Q.Q., A.G.G. and F.S. conceived the ideas and designed methodology; N.K., F.S. collected the data; N.K. analyzed the data; N.K., F.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Additional Information

Supplementary information accompanies this paper at https://doi.org/10.1038/s41598-019-38662-z.

Competing Interests: The authors declare no competing interests.

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No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring

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Summary

1. The deployment of electronic devices on animals is rapidly expanding and producing leapfrog advances in ecological knowledge. Even though their effects on the ecology and behaviour of the marked subjects are potentially important, <10% of the studies are accompanied by an evaluation of impact, and comprehensive, long-term assessments have been few. Therefore, there is an urgent need to test for impacts, especially for tags that are heavy and deployed for long time periods, such as satellite transmitters.

2. We marked 110 individuals of a medium-sized, migratory raptor, the black kite *Milvus migrans*, with GPS satellite tags, representing about 4% of the body mass and attached as backpacks through a Teflon harness. Tagged individuals were compared to control animals of similar sex, age and breeding status for a large number of behavioural, condition-related and ecological traits.

3. Despite a sample size two- to threefold greater than most previous assessments that reported significant impacts, there was no detectable difference between tagged and control individuals in key vital rates such as survival probability, longevity, recruitment, age of first breeding, reproductive performance and timing of breeding.

4. Tagged and untagged kites showed similar social dominance during fights over food and a similar capability to provision nestlings, which prevented carry-over effects on the stress levels and condition of their offspring.

5. Synthesis and applications. Radio-marking studies are growing exponentially in the current 'movement ecology era', and impact assessments will be ever more important. In principle, tags of up to 4% mass-load can be deployed without apparent harm on some avian soaring species, but impacts should be properly evaluated on a case-by-case basis. Resilient species for which impacts seem weak could be used as early warning systems for trials of new devices: if impacts are observed, they are likely to be even greater on more vulnerable species. Finally, individual fatalities caused by marking should be taken into serious account, but comprehensively evaluated in the light of broader population-level impacts. Future initiatives to minimize tagging impacts could include more stringent licensing criteria enforcing attendance at training courses or incorporation of impact evaluations into study designs, increased availability of training courses for tagging, and enhanced sharing of information through blogs, workshops or specialized journal sections.

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Key-words: backpack attachment, GPS, harness, impact, *Milvus migrans*, movement ecology, radiomarking, satellite tagging, telemetry, vital rates

Introduction

The deployment of electronic data loggers such as radiotransmitters or geolocators is increasing greatly in animal ecology as a result of the rapid improvement in device size and cost, as well as the quality of the information obtained (Cooke et al. 2004; Wikelski et al. 2007; Rutz & Hays 2009). These new technologies are producing leapfrog advances in ecological knowledge and research opportunities. For example, satellite and GSM transmitters currently facilitate an unprecedented capability to monitor animal movement, behaviour and survival for several years over enormous areas (e.g. McGrady et al. 2003; Klaassen et al. 2013; Dodge et al. 2014). In turn, this facilitates estimates of migratory performance, survival rates and causes of mortality only dreamt of until very recently, as the biases generated by poor sampling of unpopulated, remote or inaccessible areas are virtually removed (e.g. Croxall et al. 2005; Burnham & Newton 2011; Klaassen et al. 2013). However, several recent studies have shown that marking animals with devices may alter their behaviour, energetics and vital rates (reviews in Calvo & Furness 1992; Murray & Fuller 2000; Godfray & Bryant 2003; Barron, Brawn & Weatherhead 2010). Commonly reported effects include higher energy expenditures and impaired foraging, survival and breeding success, with impacts varying among species or methods of device attachment, and becoming more evident under harsher environmental conditions (e.g. Marzluff et al. 1997; Barron, Brawn & Weatherhead 2010).

These known effects of marking emphasize the need to ensure that new devices do not affect the welfare of the study subjects or prejudice the quality of the data that they are designed to obtain by influencing behaviour (e.g. Casper 2009; Kenward 2001). However, <10% of studies based on marking devices incorporate an assessment of their potential impact on the subjects and this frequency has not increased through time (Murray & Fuller 2000; Godfray & Bryant 2003). This is particularly worrying for four reasons.

1. Rapid technological developments cause researchers to 'jump' on new-generation, cutting-edge devices and this is often not accompanied by proper testing of impacts because of the pressure to produce novel results quickly.

2. Heavier devices, such as satellite or GSM tags, produce very attractive information at high costs, which leads to small samples of tracked animals that are frequently hard to capture. This leads to studies in which researchers want to maximize battery life (and thus device load) to optimize costs and field effort, but are unable to test for deleterious effects because of small samples (usually <7-10 individuals).

3. Indications of maximum admissible mass-loads are often vague, arbitrary, or based on few assessments, which makes many researchers lax about them. For example, in birds maximum suggested loads vary from 1% to 5%, with no clear agreement (e.g. Murray & Fuller 2000; Kenward 2001; Barron, Brawn & Weatherhead 2010).

4. Finally, most evaluations have examined a small set of short-term life-history parameters, which makes it unclear whether the demonstrations of low impact could be caused by the short duration of the assessment or by compensatory behaviours by the subjects (e.g. higher breeding performance at the expense of longer-term survival, or impact compensated for by higher foraging effort by an untagged partner; Barron, Brawn & Weatherhead 2010).

For all the above reasons, there is an urgent need to accompany radio-marking studies with comprehensive evaluations of their tagging impacts, in order to ensure a critical mass of results essential to produce robust metaanalyses and generalizations, as strongly requested in all recent reviews of the subject, which lament the lack of information (Calvo & Furness 1992; Murray & Fuller 2000; Barron, Brawn & Weatherhead 2010). Here, we take advantage of a long-term demographic study on a long-lived raptor, the black kite Milvus migrans, to test the impact of a large-scale satellite-marking programme (Sergio et al. 2014) on an unusually comprehensive suite of behavioural and life-history traits. The black kite is a medium-sized, opportunistic, migratory raptor. Kites are sexually monomorphic in size, but females are 15% heavier on average than males (Sergio et al. 2007a). The age of first breeding varies between 1 and 7 years, and the maximum known longevity is 28 years (Sergio et al. 2011a). We consider our study of general interest for the evaluation of tagging impacts for five reasons.

1. Transmitters were attached as backpacks using harnesses, which allow a longer period of radiodeployment, but can cause injuries (Kenward 2001), and their use is likely to spread as tags become longer-lasting.

2. Harness attachments have been shown occasionally to cause severe injuries in a threatened, congeneric and morphologically similar species, the red kite *Milvus milvus*, but no assessment of an overall population impact could be conducted (Peniche *et al.* 2011).

3. The black kite is one of the commonest soaring migrants (Newton 2008), so that information on potential data biases produced by satellite tagging could be relevant for other tracking studies on migration.

4. Satellite tags, such as those used here, are on average heavier and larger than other transmitters, but their impact has seldom been evaluated (e.g. Phillips, Xavier & Croxall 2003; Therrien, Gauthier & Bêty 2012), usually

because their high costs mean that too few animals are marked for meaningful comparisons to be made.

5. The incorporation of a large-scale tagging programme into a long-term intensive demographic study provides an ideal setting for a detailed evaluation of impact on a comprehensive suite of vital parameters, preventing the possibility that compensatory behaviours obscure real impacts.

Materials and methods

FIELD PROCEDURES: TRAPPING, SATELLITE TAGGING AND POPULATION MONITORING

We trapped 92 adult kites for radiomarking by cannon-netting them on baited carrion between March and June 2007–2013 in Doñana National Park (south-western Spain). In addition, we tagged 18 nestlings (each from a different nest) in their last week before fledging (40- to 48-day-old nestlings; Viñuela & Bustamante 1992). Kites were marked with GPS satellite tags (model PTT-100 Solar Argos/GPS PTT of 22 g, manufactured by Microwave Telemetry, Inc., Columbia, MD, USA), by attaching them as backpacks through a 6-mm-wide tubular Teflon harness (Kenward 2001). The cumulative mass of the tag and complete harness was 29.8 g, that is 3.77% of the mass of the marked kites.

More than 4000 black kites have been banded as nestlings in Doñana National Park since the 1970s, so that a large proportion of the population is composed of intensively monitored, knownage individuals, whose plastic rings can be read from far with a telescope (e.g. Blas, Sergio & Hiraldo 2009; Sergio, Blas & Hiraldo 2009a; Sergio et al. 2011a). Each year, we collected large numbers of ring readings for the whole population throughout the breeding season by regularly observing kites at their territories, at communal roosts and at trapping sites baited with carrion (Blas, Sergio & Hiraldo 2009; Sergio, Blas & Hiraldo 2009a; Sergio et al. 2009b, 2011a). This constantly high ring-reading effort allowed us to follow the fate of all ringed and satellite-tagged individuals even after the satellite tags stopped working. The nests of all breeding individuals were checked approximately every 2 weeks to estimate their breeding performance. Whenever possible, we ringed the nestlings of all pairs with a marked parent when they were approximately 35-40 days old and measured their body mass to the nearest 5 g, tarsus length to the nearest 0.1 mm, and wing length to the nearest 1.0 mm. Nestling age at ringing was estimated through a linear regression equation of chick age on the length of the eighth primary feather (Viñuela & Bustamante 1992). For each nestling, we collected two supracaudal feathers from the rump to estimate stress levels through subsequent corticosterone analysis, following the same procedures detailed by Bortolotti et al. (2008) and López-Jiménez et al. (2015). All birds trapped as adults or ringed as nestlings were sexed by molecular analysis of a blood sample.

To examine the impact of tagging on the capability to monopolize food in a competitive social environment (social dominance), we conducted standardized observations of individuals feeding and fighting on baited carrion (hereafter 'feeding observations'; Sergio *et al.* 2011b). In each observation session, we placed 30-35 skinned sheep heads of equal dimensions in a 10×10 m quadrat. Once a marked individual was feeding on a bait item, an observer placed in a hide *c.* 10 m away recorded for 10 min: (i) the number of times it was attacked by other individuals

trying to displace it from the food and their success; (ii) if displaced, the number of times it attacked other individuals to displace them and their success; and (iii) the cumulative proportion of time spent eating (i.e. the time it managed to monopolize food in a competitive environment) (Sergio *et al.* 2011b).

To estimate the effect of tagging on ability to provision offspring, we placed camera traps at 20 nests (N = 68 complete days of data): 10 nests with a satellite-tagged male and 10 nearby control nests with an untagged male. We focused exclusively on males, because in our population they are the main and almost sole providers of food for the nestlings (Sergio *et al.* 2007a). All camera traps had an infrared sensor that triggered the camera whenever it detected movement in the nest. This allowed us to record all the prey items delivered and fed to the nestlings by the parents.

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSES

To estimate the impact of tagging, each satellite-marked kite (hereafter 'satellite individual') was compared to a control individual that (i) was ringed but untagged, (ii) was of the same sex as the satellite kite, (iii) had the same age and breeding status (breeder or floater) in the year of trapping of the satellite kite (i.e. the history of the two birds was aligned to start from the same year and the same age and status conditions), and (iv) bred within the same general area of the park, if it was a breeder (i.e. within the same sector, as defined in Sergio et al. 2011c). In the few cases in which the age condition could not be satisfied, we looked for the next closest individual available and alternated equally between younger and older control birds in order to minimize age biases. Thus, for example, if control individuals of the exact same age were not available for two satellite kites of age xand y, for the first we chose a control individual of age x + 1and for the second an individual of age y-1. Because control birds had not been trapped, we defined the year of trapping of their satellite counterpart as the year of their (virtual) trapping.

Survival of satellite and control individuals was estimated using capture-recapture models (Burnham et al. 1987). Analyses were run separately for breeding and floating individuals to test whether tagging affected the two groups in different ways. Within each group, we followed the same age-structure retained by an information-theoretic approach in the detailed capture-recapture models reported in Sergio et al. (2011a), with ageclasses of 1, 2 and 3-6 years old for floaters and of 3-6, 7-11 and 12-28 years old for breeders. The statistical relevance of carrying a satellite tag was assessed using a likelihood ratio test (LRT) between a model assuming an effect of the tag and a model assuming the same survival probability for tagged and untagged kites (Burnham et al. 1987). A LRT was preferred to the model information approach based on Akaike Information Criterion (AIC) because we were interested only in testing the effect of the tag. For an extensive description of modelling kite survival, we refer to Sergio et al. (2011a).

For all other analyses, we used generalized linear mixed models (GLMMs; Zuur *et al.* 2009) to test the impact of tagging on vital rates and behaviour. Year, individual identity, or nest identity were fitted as random factors to control for pseudoreplication or for their potentially confounding effect (Table 1). In all models, we were interested in testing the following predictions: (i) behavioural and demographic performance are lower in tagged than in control individuals; (ii) such impacts are stronger in certain

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Table 1. Hypotheses and	predictions of the impact	t of satellite taggin	g on several life-history,	, ecological and	behavioural	traits of individ-
ual black kites						

Trait tested for impact ^a	Explanatory variables ^b	Hypothesis Tagging affects:	Prediction Significant effect of:
a. Adult mass	Tagging, sex, age, date,	The body mass of the radio-marked adult	Tagging
	time-lag from 1st trapping ^c	Adult body mass depending on sex	Tagging \times sex
		Adult body mass depending on age	Tagging \times age
		Adult body mass, but its effect increases with time	Tagging \times time-lag
b, c. Survival ^d	Tagging, sex, age	Survival	Tagging
		Survival depending on sex	Tagging \times sex
		Survival depending on age	Tagging \times age
d. Longevity	Tagging, sex, status,	Longevity	Tagging
	age at trapping ^{e,f}	Longevity depending on sex	Tagging \times sex
	0 11 0	Longevity depending on status	Tagging \times status
		Longevity depending on age at tagging	
e. Recruitment ^g	Tagging, sex, age ^c	Annual recruitment ^g	Tagging
		The recruitment of floaters depending on sex	Tagging \times sex
		The recruitment of floaters depending on age	Tagging \times age
f. Recruitmenth	Tagging, sex, age at trapping ^f	Cumulative recruitment ^h	Tagging
		The recruitment of floaters depending on sex	Tagging \times sex
		The recruitment of floaters depending on age at tagging	Tagging \times age
g. Age at 1st	Tagging, sex, age at trapping ^f	Age at first breeding (age 1st breed)	Tagging
breeding		The age 1st breed of floaters depending on sex	Tagging \times sex
		The age 1st breed of floaters depending on age at tagging	Tagging \times age
h,i,j.	Tagging, period ^j , sex, age ^c	Productivity ^j	Tagging \times period
Productivity ⁱ		Productivity ^j depending on sex	Tagging \times period \times sex
		Productivity ^j depending on age	Tagging \times period \times age
k,l. Social	Tagging, sex, age, date	Social competence ^k	Tagging
competencek		Social competence ^k depending on sex	Tagging \times sex
		Social competence ^k depending on age	Tagging \times age
m. Provisioning	Tagging, age ^l , date,	Nestlings provisioning rates	Tagging
rates	brood size, nestling age	Provisioning rates depending on parental age	Tagging \times age
		The provisioning rates at broods of 1 vs. 2 nestlings	Tagging \times brood size
n. Nestlings'	Tagging, age, brood order,	Nestlings' body mass at ringing	Tagging
body mass	nestling age, tarsus length	Nestlings' mass depending on sex of the marked parent	Tagging \times sex
-		Nestlings' mass depending on age of the marked parent	Tagging \times age
o. Nestlings'	Tagging, age, brood order,	Nestlings' feather-corticosterone levels (Cort)	Tagging
Cort ^m	chick age, chick condition ⁿ	Nestlings' Cort depending on sex of the marked parent	Tagging \times sex
		Nestlings' Cort depending on age of the marked parent	Tagging \times age

^aDependent variable in each model. The letters that identify each model (a, b, c, etc.) correspond to those in Table 2.

^bExplanatory variables fitted to the model to control for confounding factors that could obfuscate the effect of tagging (the interactions fitted to each model are specified in the column 'Prediction').

^cIndividual identity and year were fitted as random factors.

^dSurvival of both floaters and breeding kites: the hypotheses and predictions were the same for both models.

^eBreeding status (1 = floater, 2 = breeder).

^fIndividual identity was fitted as a random factor.

^gAnnual recruitment: probability that a floater will recruit in a given year.

^hCumulative recruitment: whether a floater recruited or died within 7 years of age.

ⁱIncludes models with laying date, clutch size or number of fledged young as dependent variables.

^jBreeding attempts before or after the tagging episode. The inclusion of this variable allowed to test whether differences in productivity between satellite and control individuals before tagging were amplified or reduced after radiomarking.

^kIncludes models with the capability of fighting or of monopolizing food in a competitive social group as dependent variables.

¹Age of the parent bird. Sex was not fitted because the analysis focused exclusively on males (the main food-providing sex).

^mCorticosterone levels in feathers (pg mm⁻¹).

ⁿResiduals of a regression of the nestlings' body mass on their age and tarsus length.

ageclasses (e.g. in younger inexperienced individuals, or in older birds because of the added cost of breeding); and (iii) tagging impacts are stronger in males because they receive larger loads due to their lower mass and have higher metabolic costs during breeding as they are the main food providers for the whole family. Therefore, we fitted to all models the variable 'tagging' (whether an individual was a satellite or control kite) and its interaction with age and sex. Other covariates included in the models are detailed in Table 1 and were chosen based on accumulated knowledge about the study population in order to control for confounding factors potentially affecting each dependent variable and thus obfuscating tagging effects.

To analyse the impact of tagging on longevity, we proceeded as follows: capture–recapture models provided an estimate of recapture probability for untagged birds, defined as the probability to resight a bird at a specific time *i*, given that it has survived Table 2. GLMM and capture-recapture models testing the impact of satellite tagging on the body condition, vital rates, social dominance and the capability of adequately provisioning the offspring by black kites. All analyses are based on the comparison of satellite-tagged kites and control individuals of the same sex, age and site quality (see Materials and methods)

Variable	n	ΔAkaike Information Criterion (AIC) ^a	LR test ^b	Р
a. Dependent variable: adult body mass ^{c,d}	46			
Tagging ^e		-1.78	0.23	0.63
Tagging \times sex		-1.86	0.14	0.72
Tagging \times age		-1.91	0.08	0.78
Tagging \times time-lag ^f		-1.73	0.27	0.60
h Dependent variable: survival floaters ^g	$80^{\rm h}$	1,0	0 = /	0.00
Tagging ⁱ	00	-1.01	1.15	0.28
Tagging X sev		1.63	0.65	0.42
Tagging × sex		3.02	0.62	0.73
Denendent meister mensionel have deneg	114 ^h	-3.92	0.02	0.73
Transie d	114	0.26	1.00	0.16
Tagging		-0.26	1.99	0.10
$lagging \times sex$		-8.22	1.64	0.95
Tagging \times ageclass		-0.26	1.99	0.16
d. Dependent variable: longevity ¹	48			
Tagging		-1.98	0.01	0.92
Tagging \times sex		-2.00	<0.01	0.99
Tagging \times status ^k		-1.85	0.15	0.70
Tagging \times age ¹		-1.89	0.11	0.74
e. Dependent variable: annual recruitment ^m	80 ⁿ			
Tagging ⁱ		-1.99	0.01	0.92
Tagging \times sex		-1.95	0.05	0.82
Tagging × ageclass		-1.58	1.42	0.23
f Dependent variable: cumulative recruitment ^m	42°	1 50	1 72	0 25
Tagging ¹	42	1.02	0.08	0.78
		1.01	0.08	0.78
		-1.91	0.09	0.77
Lagging \times ageclass	16	-1.84	0.10	0.69
g. Dependent variable: age of first breeding	46			
Tagging		-1.99	0.01	0.94
Tagging \times sex		-1.99	0.01	0.92
Tagging \times age ¹		-1.95	0.04	0.84
h. Dependent variable: Laying date ^d	126			
Tagging ⁱ		-1.82	0.18	0.67
Tagging \times period		-3.96	0.04	0.98
Tagging \times period \times sex		-1.88	0.13	0.72
Tagging \times period \times age		-0.14	1.86	0.17
i. Dependent variable: Clutch size ^j	128			
Tagging ⁱ		-1.97	0.03	0.86
Tagging x period		-1:63	0.37	0.55
Tagging \times period \times sex		-5.22	0.78	0.85
Tagging \times period \times age		10.43	1.57	0.05
i Dependent variable: number of fladged voung	200	-10.43	1.37	0.75
J. Dependent variable, number of nedged young	200	1 (5	0.24	0.50
		-1.03	0.34	0.30
$lagging \times period$		-1.98	0.02	0.89
Tagging \times period \times sex		-4.90	1.10	0.78
Tagging \times period \times age		-5.47	0.53	0.91
k. Dependent variable: social dominance ^{d,p}	48			
Tagging ¹		-2.01	0.01	0.99
Tagging \times sex		-1.21	0.79	0.37
Tagging \times ageclass		-2.82	1.18	0.55
l. Dependent variable: fighting capability ^{d,q}	48			
Tagging ⁱ		-1.69	0.31	0.58
Tagging \times sex		-1.99	0.01	0.93
Tagging \times ageclass		-3.24	0.77	0.68
m Dependent variable: nestling provisioning rates ^{d,r}	68		/	0.00
Tagging ⁱ	00	-1.95	0.04	0.84
Tagging × brood size		1.83	0.16	0.04
Tagging × agoalass		-1.05	0.84	0.00
ragging × ageciass		-1.10	0.94	0.36

(continued)

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Table 2. (continued)

Variable	п	ΔAkaike Information Criterion (AIC) ^a	LR test ^b	Р
n. Dependent variable: nestlings' body mass at ringing ^d	78			
Tagging ⁱ		-1.95	0.05	0.82
Tagging \times sex ^s		-4.22	1.78	0.62
Tagging \times ageclass		-5.29	2.71	0.61
o. Dependent variable: nestlings' corticosterone levels ^d	58			
Tagging ⁱ		-1.93	0.08	0.78
Tagging \times sex ^s		-1.78	0.22	0.64
Tagging \times ageclass		-2.14	1.86	0.39

^aChange in AIC value when removing the variable from the maximal model (see Materials and methods). Negative values indicate that the model fit improved upon removal of the variable from the model. In all cases, the same results were obtained when adding the variable to the minimal model or to the null model.

^bLikelihood ratio test of the change in deviance upon removal of the variable from the maximal model.

^cBody mass of individuals that were recaptured later in life after radiotagging.

^dLinear mixed model with Gaussian errors and an identity link function.

Tagging treatment: for this model, 1 = measurement at first capture (i.e. just before radiotagging); 2 = measurement (without radiotag) upon its recapture later in life.

^fTime-lag between the first and second capture of the same individual.

^gSurvival models were implemented in MARK for individuals captured as breeders or as floaters (i.e. non-breeding individuals).

^hFloaters: N = 40 satellite-tagged vs. 40 control individuals; breeders: N = 57 satellite-tagged vs. 57 control individuals.

ⁱTagging treatment: 1 = satellite-tagged bird; 2 = control individual. ^jGeneralized linear mixed model with Poisson errors and a logarithmic link function.

^kBreeding status at capture: 1 = floater; 2 = breeder.

¹Age at the time of tagging.

^mGeneralized linear mixed model with binomial errors and a logit link function.

ⁿAnalysis based on N = 192 recruitment episodes (each year in which a previously floater individual was known to be alive and either recruited or not) from 40 satellite-tagged vs. 40 control individuals.

°Analysis based on N = 21 satellite-tagged vs. 21 control individuals which recruited or not within their initial 7 years of life.

^pCapability to monopolize food in a competitive social group, as estimated by the proportion of time spent eating in a group of conspecifics during 10-min bouts of observation (arcsine square-root transformed).

^qProportion of times that an individual succeeded in either dislodging another individual from a food item or to defend it from an attacker (arcsine square-root transformed).

^rBiomass of prey delivered to the nestlings per day (N = 68 full days of camera-trapping from 10 nests of satellite-tagged males and 10 nests of control individuals).

^sSex of the parent individual.

the previous time interval, from i-1 to i. In particular, the detection probability of untagged birds was 0.97 per year for breeding kites and 0.72 for non-breeding kites. Thus, the probability that an unmarked breeding bird estimated to be alive was in the population for two consecutive years without being seen was very low at $(1-0.97)^2 = 0.0009$. This figure was 0.08 for a non-breeding kite and dropped to 0.02 for a bird not seen for three consecutive years. Based on the above, we classified an individual as dead if it was (i) physically recovered as such, (ii) a breeder not seen for two consecutive years or (iii) a non-breeder not seen for three consecutive years. For individuals classified as dead according to the above criteria, we then examined the effect of carrying or not a satellite tag on observed longevity, defined as the age of an individual when it was classified as dead (i.e. its age when last observed; Table 1). All individuals of uncertain status (e.g. not seen for only 1 year) were discarded from analysis.

Similarly, because the detectability of breeders was extremely high, we classified a bird as recruited if it was observed holding a territory and as a floating bird if it was known to be alive that year (e.g. because it was regularly observed at roosts, or seen alive in subsequent years) but was never observed holding a territory. Non-recruited individuals not observed for 3 years or more at the end of the study or not observed in the final 2 years of the study were discarded from recruitment analyses because they were estimated as dead (see above), or to avoid biasing results by including false zeros (i.e. individuals that could appear as still alive in subsequent years). We then explored the effect of tagging on the probability that a floating individual would recruit or not in each individual year in which it was known to be alive (defined as 'annual recruitment'; Table 1). To provide a longer-term and more comprehensive measure of recruitment efficacy, we also tested whether tagging affected the probability that an individual would recruit within its first 7 years of life (7 years is the maximum age of first breeding in our population; Sergio, Blas & Hiraldo 2009a). We define this as 'cumulative recruitment' and included in this analysis: (i) individuals known to have recruited; and (ii) individuals that were unknown to have recruited but would have reached 7 years of age within the end of the study. Therefore, each individual appeared only once in this analysis.

For estimates of reproductive timing and success, data were also available for the longitudinal performance of each satellite and control individual before and after the tagging year (not available for other traits because, for example, survival is 1 by default before trapping). This allowed us to implement a full before–after control–impact (BACI) test by checking whether the performance was similar between the two groups both before and after tagging. Thus, in these analyses, an impact of satellite marking was revealed by a significant interaction between 'tagging' (whether an individual was a satellite or control kite) and 'period' (i.e. before vs. after 'the tagging year', Table 1; see Gregory, Gordon & Moss 2003 for a similar design).

For feeding observations, it was often impossible to find adequate control individuals of the same age within the few hours of each observation day. So, whenever a satellite-tagged individual was present, we recorded its performance and compared it to the one of the ringed, untagged individual observed just before or after the tagged focal individual. Age was then controlled simply by fitting it as a covariate. Similarly, for nest provisioning rates, we opportunistically chose as control nest a nearby one occupied by a ringed untagged male.

In Table 1, we give details of the explanatory variables fitted to the models, and of the hypotheses and predictions testing the impact of tagging. All models were built through a backward stepwise procedure following Zuur *et al.* (2009): all explanatory variables were fitted to a maximal model, extracted one at a time from such maximal model, and the associated change in model deviance was assessed by a LRT; at each step, we also calculated the AIC of each model and considered as the final competitive model the one with the lowest AIC containing only significant terms. Variables with a $\Delta AIC < 2$ upon removal or with P > 0.05in the LRT were considered as non-significant.

In all analyses, age was fitted as a linear, quadratic or categorical variable (with levels: 1-2, 3-6, 7-11 and 12-27 years old), based on which gave the best fit to the maximal model, as detailed in Sergio et al. (2014). Details of the error distribution of each model are given in the footnotes of Table 2. In all models, we assessed collinearity by examining the variance inflation factor (VIF) values of the explanatory variables, which were always low (<1.3; Crawley 2007; Zuur et al. 2009). To avoid over-parameterization, we ensured never to fit more than N/3 variables to each maximal model (Crawley 2007). Overdispersion was never detected and model assumptions were checked by looking at QQ plots, histograms of residuals, and plots of standardized and normalized residuals against fitted values and against explanatory variables, or by incorporating variance structures VarIdent or VarFixed (Crawley 2007; Zuur et al. 2009). All GLMMs were implemented in R 3.0.2 (R Development Core Team 2009) and all capture-recapture models in MARK (White & Burnham 1999). All tests are two-tailed, statistical significance was set at $\alpha < 0.05$, and all means are given ± 1 SE.

Results

A single individual removed its harness 4 months after marking (0.9% of 110 tagged individuals). Of 42 individuals retrapped or recovered freshly dead up to 4 years after tagging, one had an abrasion below the ventral T-junction of the harness, caused by an unusually tightfitting ventral loop of the harness, similar to that described by Sunde (2006), but less severe than the injuries reported by Peniche *et al.* (2011). The retrapped bird was freed from the incorrectly placed harness and went on to successfully raise young. In all the recovered birds, the skin under the transmitter was always featherless but intact, with no sign of inflammation or previous injury. No other signs of injury were evident and the body mass of the tagged birds was similar at marking and when retrapped, independently of the time-lag between the two (Table 2a; Fig. 1).

For both breeding and non-breeding kites, there was no difference in the survival of tagged and control individuals, and no significant interaction between marking treatment and age or sex (Table 2b,c; Fig. 2). The duration of the study prevented a similar analysis for birds tagged as nestlings, but the remotely recorded survival of the satellite birds to 1 year of age was 0.421 ± 0.116 (N = 18), that is similar to the 0.407 estimate based on ring recoveries for the same population (Sergio *et al.* 2011a). For birds that died during the course of the study, there was no difference in mean longevity between tagged and control individuals, independently of their age or sex (Table 2d; Fig. 3).

The annual and cumulative recruitment of floating kites into the breeding population and their age of first breeding were not affected by tagging, nor by its interaction with age or sex (Table 2e,f,g; Figs 2 and 3). Similarly, laying date, clutch size and the number of young raised to fledging did not vary with tagging or its interaction with age or sex (Table 2h,i,j; Fig. 4).



Fig. 1. Body mass of 23 adult black kites when trapped for satellite tagging and of the same 23 individuals upon retrapping after radiotagging. Bars represent means +1 SE.



Fig. 2. Survival and recruitment rates of satellite-tagged black kites (grey bars) and control individuals (white bars). Annual recruitment is the probability that a floater will recruit in a given year, while cumulative recruitment is the probability that it will recruit within its seventh year of life. Bars represent mean +1 SE.

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Fig. 3. Age of first breeding and longevity of satellite-tagged black kites (grey bars) and control individuals (white bars). Bars represent mean +1 SE.

The proportion of time spent eating carrion, the capability to evict other kites from a food item or to defend it, and nestling provisioning rates did not differ between satellite and control birds (Table 2k,l,m; Figs 5 and 6). Finally, the body mass at ringing and the corticosterone levels of the nestlings did not vary with the tagging of their parents or its interaction with parental age or sex (Table 2n,o; Fig. 6).

Discussion

We found no evidence of a marked impact of satellite tagging on black kites. Social dominance over food and foraging performance, as assessed by provisioning rates, were unaffected by tagging, suggesting that the added load and drag did not excessively impair flight capabilities. As a result, the body mass of marked birds was maintained, even after several years of wearing a tag. Similarly, key vital rates, such as survival, recruitment, age of first breeding and reproductive success, were not related to marking, which ultimately resulted in similar longevities between satellite and control individuals. Finally, tagging did not delay reproduction or reduce the condition of raised offspring. All the above relationships were independent of the age, sex, or status of the marked animal, suggesting that there were no socio-ecological characteristics which made an individual more prone to suffer a cost of tagging. In summary, there was no evidence of an impact on foraging and social behaviour, on the capability to proceed through key life stages and survive to breed, and no apparent carry-over effect on the viability of the offspring produced.

We doubt that the above results could be artefacts for five reasons.

1. The magnitude of all differences between satellite and control kites was so small and the overlap in measures of variation so large, that only a very extreme data bias could have reversed the results. We cannot think of such a source of bias. In fact, if anything, satellite kites performed slightly better than control individuals in many key comparisons, as reported in a recent meta-analysis (Barron, Brawn & Weatherhead 2010).



Fig. 4. Timing of breeding (a), clutch size (b) and number of young raised to fledging age (c) by satellite-tagged black kites (grey bars) and control individuals (white bars), before and after being trapped and radio-marked. Bars represent mean +1 SE.

2. The sample size and duration of the study were two- or threefold larger than those of most previous studies that did detect significant impacts (reviews in Calvo & Furness 1992; Murray & Fuller 2000; Barron, Brawn & Weatherhead 2010).

3. Compared to previous evaluations, the study was unusually comprehensive in testing differential impacts by sex, age and breeding status on a larger than usual set of vital parameters and behaviours.

4. The systematic absence of impact in the whole comprehensive set of parameters analysed does not support the possibility that behavioural compensation obscured impacts by relegating them to unmeasured parameters. For example, there was no evidence that the absence of a



Fig. 5. Social competence of satellite-tagged black kites (grey bars) and control individuals (white bars). Social dominance was the ability to monopolize food in a competitive social group, and fighting capability was the percentage of successful defensive and offensive interactions with conspecifics over food. Bars represent mean +1 SE.



Fig. 6. Prey provisioning rates by adults to their nestlings (grams of prey delivered per day), and offspring body mass (in grams) and corticosterone (Cort) levels in feathers ($pg mm^{-1}$) for nests of satellite-tagged black kites (grey bars) and control individuals (white bars). Corticosterone levels were multiplied by 50 for clarity of presentation. Bars represent mean +1 SE.

tag effect on survival was attained through lower breeding effort or that sustained breeding success was maintained at the expense of offspring condition. A similar absence of compensatory mechanisms has been suggested by a recent meta-analysis (Barron, Brawn & Weatherhead 2010).

5. Finally, in the presence of a tagging impact, we would expect the performance of marked birds to deteriorate progressively through the years, as cumulative deleterious effects become more evident. On the contrary, most individuals improved their performance in successive years (as they aged and accumulated experience) in the same ways and with the same outcomes that had been previously described for ringed but non-radio-tagged kites of the same population. Thus, for example, individuals arrived progressively earlier at the breeding quarters in successive years and this translated into advantages for recruitment and reproduction (Sergio *et al.* 2007b; Sergio, Blas & Hiraldo 2009a; Sergio *et al.* 2014). Therefore, tagging did

not prevent us from capturing a realistic snapshot of the demographic functioning and life-history strategies of the population. All in all, if tagging effects were present in our population, they were likely to be of very limited magnitude and difficult to detect over the analysed time period.

Previous evaluations of the impact of backpack transmitters on birds of prey have reported significant effects on breeding performance (Foster et al. 1992; Marzluff et al. 1997; Gregory, Gordon & Moss 2003; Rodríguez et al. 2009) or on survival (Gervais et al. 2006; Steenhof et al. 2006), or both (Paton et al. 1991), or no detectable effect on breeding (Vekasy et al. 1996; Sunde 2006; Therrien, Gauthier & Bêty 2012) or survival (Foster et al. 1992; Reynolds et al. 2004; Sunde 2006; Rodríguez et al. 2009). Note that evaluations of satellite impacts have been almost nonexistent (Steenhof et al. 2006; Therrien, Gauthier & Bêty 2012), despite much marking. Our results confirm that satellite marking may not be particularly deleterious in some cases. However, we express extreme caution in extrapolating the results of this study uncritically to other species for several reasons. First, the black kite has been defined as the paradigm of the generalist species (Viñuela 2000); it can kill prey ranging from a mosquito to a live 1kg adult rabbit Oryctolagus cuniculus (authors' pers. obs.) and is considered to be the most numerous and successful raptor in the world (Ferguson-Lees & Christie 2001). As such, it may be better able to absorb the impact of tagging than others less generalist species. Secondly, it is a migratory, highly opportunistic predator adapted to exploit sudden flushes of food and to withstand periods of prey scarcity (Viñuela 2000). Its body mass thus fluctuates widely, with recorded mass variations of more than 250 g within individuals over the course of a few months (Sergio et al. 2009b; authors' unpublished data), that is more than eight times the tagging load. This may make this species well pre-adapted to withstand load additions. Thirdly, black kites are soaring migrants dependent on thermals (Newton 2008) and the breeding and wintering quarters of the study population are located in arid or semi-arid, generally warm areas, where thermal uplift may be common and strong, thus dampening the energetic costs of carrying an additional load. Other species or even other black kite populations that breed in colder climates and experience longer migrations could show larger impacts. Lastly, cumulative effects may only be visible over even longer time periods, through longer-term assessments that will only be available in future years as our study continues.

CONCLUSIONS AND APPLICATIONS

Although radiotagging may be sufficiently harmless in some contexts, even for transmitter loads up to almost 4% of body mass, evaluations of impact will be increasingly important as progressive improvements in device costs and miniaturization broaden the range and abundance of tagged species (e.g. Wikelski *et al.* 2007). In

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the future, resilient species or populations like ours could be used as 'early warning systems' to test the viability of different transmitter types and loads because, if impacts are observed in these model species, they will be even more likely to occur in more exacting species. This could minimize unethical impacts and waste of funds and data in projects on threatened or more delicate taxa. Finally, the only adverse effect observed in this study was caused by one misplaced, excessively tight-fitting harness. This finding raises two issues. First, radiomarking through harnesses is likely to become more common because it is conducive to longer-term deployment and researchers will increasingly fit tags capable of functioning for years, yet harness-fitting is known to require experienced personnel (Kenward 2001) as poor practice can be harmful (e.g. Peniche et al. 2011). Secondly, mistakes are probably inevitable in any marking programme (Kenward 2001) and, however dramatic individual instances may be, decisions about the suitability of methods should be accompanied by broader assessments of comprehensive demographic impacts. Consequently, because occasional casualties or harm directly or indirectly caused by marking can have an impact with the public, it is important that scientists can provide explanations based on quantitative assessments, rather than qualitative reasoning.

Various initiatives could help to improve the issues raised above. First, tagging licences could be issued through more stringent criteria, such as demonstration of attendance at training courses, previous successful experience with the technique, or explicit incorporation of an impact evaluation into the project design. Secondly, highquality training should be enhanced through more specialized courses (e.g. at congresses). Thirdly, sharing of information among users should be fostered through specialized blogs, forums or workshops, or by creating ad hoc sections in journals focusing on biotelemetry and animal movement. Fourthly, journal editors could demand that authors of telemetry studies should incorporate impact evaluations into their work as an essential component of study design. Finally, for studies constrained by funding limitations to fewer than 10 tagged individuals, for which impact evaluations will be difficult, we recommend that researchers use tags weighing <3%, and preferably 1%, of the body mass, that they use tagging methods previously tested on similar species, and that they explicitly express caution about the validity of their data as impact evaluations could not be implemented. Note that, with such small samples, adverse impacts even on a single individual could have severe consequences for the reliability of the whole analysis.

Acknowledgements

We thank F.J. Chicano, F.G. Vilches, J.M. Giralt and M. Anjos for help in the field, the personnel of the Reserva Biológica de Doñana for logistical help and accommodation and Microwave Telemetry for technical support. We thank M. Whittingham, J. Wilson and two anonymous referees for constructive comments on a previous draft of the manuscript. The study received funding by Natural Research Ltd, The Spanish Severo Ochoa Program for Excellence (SEV-2012-0262) and research projects CGL2008-01781, CGL2011-28103 and CGL2012-32544 of the Spanish Ministry of Science and Innovation/Economy and Competitiveness and FEDER funds, 511/2012 of the Spanish Ministry of Agriculture, Food and the Environment (Autonomous Organism of National Parks), JA-58 of the Consejería de Medio Ambiente de la Junta de Andalucía and by the Excellence Projects RNM 1790, RNM 3822 and RNM 7307 of the Junta de Andalucía. J.B. was supported by a Ramón y Cajal contract from the CSIC.

Data accessibility

Metadata on vital rates, social dominance, provisioning and nestlings' biomass available from the Figshare Digital Repository doi:10.6084/m9. figshare.1491385 (Sergio *et al.* 2015).

References

- Barron, D.G., Brawn, J.D. & Weatherhead, P.J. (2010) Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology* and Evolution, 1, 180–187.
- Blas, J., Sergio, F. & Hiraldo, F. (2009) Age-related reproduction in a long-lived raptor: a cross-sectional and longitudinal study. *Ecography*, 32, 647–657.
- Bortolotti, G.R., Marchant, T.A., Blas, J. & German, T. (2008) Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. *Functional Ecology*, **22**, 494–500.
- Burnham, K.K. & Newton, I. (2011) Seasonal movements of Gyrfalcons Falco rusticolus include extensive periods at sea. Ibis, 153, 468–484.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. (1987). Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture. Am. Fish. Soc. Monogr. No. 5., Bethesda, MD.
- Calvo, B. & Furness, R.W. (1992) A review of the use and the effects of marks and devices on birds. *Ringing and Migration*, 13, 129–151.
- Casper, R.M. (2009) Guidelines for the instrumentation of wild birds and mammals. *Animal Behaviour*, 78, 1477–1483.
- Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G. & Butler, P.J. (2004) Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution*, **19**, 334–343.
- Crawley, M.J. (2007) The R Book. Wiley Press, Chichester.
- Croxall, J.P., Silk, J.R.D., Phillips, R.A., Afanasyev, V. & Briggs, D.R. (2005) Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science*, **307**, 249–250.
- Dodge, S., Bohrer, G., Bildstein, K., Davidson, S.C., Weinzierl, R., Bechard, M.J. et al. (2014) Environmental drivers of variability in the movement ecology of turkey vultures (*Cathartes aura*) in North and South America. *Philosophical Transactions of the Royal Society of Lon*don. Series B, Biological Sciences, 369, 20130195 1471–2970.
- Ferguson-Lees, J. & Christie, D.A. (2001) *Raptors of the World*. Houghton Mifflin Company, New York, NY.
- Foster, C.C., Forsman, E.D., Meslow, E.C., Miller, G.S., Reid, J.A., Wagner, F.F., Carey, A.B. & Lint, J.B. (1992) Survival and reproduction of radio-marked adult spotted owls. *Journal of Wildlife Management*, 56, 91–95.
- Gervais, J.A., Catlin, D.H., Chelgren, N.D. & Rosenberg, D.K. (2006) Radiotransmitter mount type affects burrowing owl survival. *Journal of Wildlife Management*, **70**, 872–876.
- Godfray, J.D. & Bryant, D.M. (2003) Effects of radio transmitters: review of recent radio-tracking studies. *Science for Conservation*, 214, 83–95.
- Gregory, M.J.P., Gordon, A.G. & Moss, R. (2003) Impact of nest-trapping and radio-tagging on breeding Golden Eagles *Aquila chrysaetos* in Argyll, Scotland. *Ibis*, **145**, 113–119.
- Kenward, R.E. (2001) A Manual for Wildlife Radio Tagging. Academic Press, London.
- Klaassen, R.H.G., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K.-M., Barlein, F. & Alerstam, T. (2013) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, 83, 176–184.
- López-Jiménez, L., Blas, J., Tanferna, A., Cabezas, S., Marchant, T.A., Hiraldo, F. & Sergio, F. (2015) Ambient temperature, body condition

and sibling rivalry explain feather corticosterone levels in developing black kites. *Functional Ecology* doi: 10.1111/1365-2435.12539.

- Marzluff, J.M., Vekasy, M.S., Kochert, M.N. & Steenhof, K. (1997) Productivity of Golden Eagles wearing backpack radiotransmitters. *The Journal of Raptor Research*, **31**, 223–227.
- McGrady, M.L., Ueta, M., Potapov, E., Uteckhina, I., Masterov, V., Ladyguine, A. et al. (2003) Movements by juvenile and immature Steller's Sea Eagles Haliaeetus pelagicus tracked by satellite. Ibis, 145, 318–328.
- Murray, D.L. & Fuller, M.R. (2000) A critical review of the effects of marking on the biology of vertebrates. *Research Techniques in Animal Ecology* (eds L. Boitani & T.K. Fuller), pp. 15–64. Columbia University Press, New York, NY.

Newton, I. (2008) The Migration Ecology of Birds. Academic Press, London.

- Paton, P.W.C., Zabel, C.J., Neal, D.L., Steger, G.N., Tilghman, N.G. & Noon, B.R. (1991) Effects of radio tags on spotted owls. *Journal of Wildlife Management*, 55, 617–622.
- Peniche, G., Vaughan-Higgins, R., Carter, I., Pocknell, A., Simpson, D. & Sainsbury, A. (2011) Long-term health effects of harness-mounted radio transmitters in red kites (*Milvus milvus*) in England. *The Veterinary Record*, 169, 311.
- Phillips, R.A., Xavier, J.C. & Croxall, J.-P. (2003) Effects of satellite transmitters on albatrosses and petrels. *The Auk*, **120**, 1082–1090.
- R Development Core Team (2009) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org.
- Reynolds, R.T., White, G.C., Joy, S.M. & Mannan, R.W. (2004) Effects of radiotransmitters on northern goshawks: do tailmounts lower survival of breeding males? *Journal of Wildlife Management*, 68, 25–32.
- Rodríguez, A., Negro, J.J., Fox, J.V. & Afanasyev, V. (2009) Effects of geolocator attachments on breeding parameters of Lesser Kestrels. *Journal of Field Ornithology*, 80, 399–407.
- Rutz, C. & Hays, G.C. (2009) New frontiers in biologging science. *Biological Letters*, 5, 289–292.
- Sergio, F., Blas, J. & Hiraldo, F. (2009a) Predictors of floater status in a long-lived bird: a cross-sectional and longitudinal test of hypotheses. *Journal of Animal Ecology*, 78, 109–118.
- Sergio, F., Blas, J., Forero, M.G., Donázar, J.A. & Hiraldo, F. (2007a) Size-related advantages for reproduction in a slightly dimorphic raptor: opposite trends between the sexes. *Ethology*, **113**, 1141–1150.
- Sergio, F., Blas, J., Forero, M.G., Donázar, J.A. & Hiraldo, F. (2007b) Sequential settlement and despotic site-dependence in a migratory raptor. *Behavioral Ecology*, 18, 811–821.
- Sergio, F., Blas, J., Baos, R., Forero, M.G., Donázar, J.A. & Hiraldo, F. (2009b) Short and long-term consequences of individual and territory quality in a diurnal raptor. *Oecologia*, **160**, 507–514.
- Sergio, F., Tavecchia, G., Blas, J., López, L., Tanferna, A. & Hiraldo, F. (2011a) Age-structured vital rates in a long-lived raptor: implications for population growth. *Basic and Applied Ecology*, **12**, 107–115.

- Sergio, F., Blas, J., Blanco, G., Tanferna, A., López, L., Lemus, J. & Hiraldo, F. (2011b) Raptor nest decorations are a reliable threat against conspecifics. *Science*, **331**, 327–330.
- Sergio, F., Blas, J., López, L., Tanferna, A., Díaz-Delgado, R., Donázar, J.A. & Hiraldo, F. (2011c) Coping with uncertainty: breeding adjustments to an unpredictable environment in an opportunistic raptor. *Oecologia*, **166**, 79–90.
- Sergio, F., Tanferna, A., De Stephanis, R., López Jímenez, L., Blas, J., Tavecchia, G., Preatoni, D. & Hiraldo, F. (2014) Individual improvements and selective mortality shape lifelong migratory performance. *Nature*, **515**, 410–413.
- Sergio, F., Tavecchia, G., Tanferna, A., López Jiménez, L., Blas, J., De Stephanis, R., Marchant, T.A., Kumar, N. & Hiraldo, F. (2015) Data from: No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. *Figshare*, http://dx.doi.org/10.6084/ m9.figshare.1491385.
- Steenhof, K., Bates, K., Fuller, M.R., Kochert, M.N., McKinley, J.O. & Lukacs, P.M. (2006) Effects of radiomarking on prairie falcons: attachment failures provide insight about survival. *Wildlife Society Bulletin*, 34, 116–126.
- Sunde, P. (2006) Effects of backpack radio tags on tawny owls. Journal of Wildlife Management, 70, 594–599.
- Therrien, J.-F., Gauthier, G. & Bêty, J. (2012) Survival and reproduction of adult snowy owls tracked by satellite. *Journal of Wildlife Management*, 76, 1562–1567.
- Vekasy, M.S., Marzluff, J.M., Kochert, M.N., Lehman, R.N. & Steenhof, K. (1996) Influence of radio-transmitters on Prairie Falcons. *Journal of Field Ornithology*, 67, 680–690.
- Viñuela, J. (2000) Opposing selective pressures on hatching asynchrony: egg viability, brood reduction and nestling growth. *Behavioral Ecology* and Sociobiology, 48, 333–343.
- Viñuela, J. & Bustamante, J. (1992) Effect of growth and hatching asynchrony on the fledging age of Black and Red kites. *The Auk*, **109**, 748– 757.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46(Supplement), 120–138.
- Wikelski, M., Kays, R.W., Kasdin, N.J., Thorup, K., Smith, J.A. & Swenson, G.W. (2007) Going wild: what a global small-animal tracking system could do for experimental biologists. *Journal of Experimental Biology*, **210**, 181–186.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R.* Springer, New York, NY.
- Received 4 December 2014; accepted 29 July 2015 Handling Editor: Jeremy Wilson

PROCEEDINGS OF THE ROYAL SOCIETY B

BIOLOGICAL SCIENCES

The population density of an urban predator is inextricably tied to human cultural practices

Journal:	Proceedings B
Manuscript ID	RSPB-2018-2932
Article Type:	Research
Date Submitted by the Author:	27-Dec-2018
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Subject:	Ecology < BIOLOGY
Keywords:	human culture, human subsidies, nest availability, population limitation, tree management, urban raptor
Proceedings B category:	Global Change & Conservation



1 2 3	The population density of an urban predator is inextricably tied to human cultural practices
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50 Abstract

51

Human socio-cultural factors are recognized as fundamental drivers of urban ecological 52 processes, but their effect on wildlife is still poorly known. In particular, human cultural 53 aspects may differ substantially between the extensively studied urban settings of 54 55 temperate regions and the poorly-studied cities of the tropics, which may thus offer profoundly different niches for urban wildlife. Here, we report how the population-56 levels of a scavenging raptor which breeds in the megacity of Delhi, the Black kite 57 58 Milvus migrans, depend on spatial variation in human subsidies, mainly in the form of philanthropic offerings of meat given for religious purposes. This tight connection with 59 60 human culture, which generated the largest raptor concentration in the world, was modulated further by breeding-site availability. The latter constrained the level of 61 62 resource-tracking by the kites and their potential ecosystem service, and could be used as a density-management tool. Similar ties between animal population-densities, key 63 64 anthropogenic resources and human beliefs may occur in thousands of cities all over the globe and may fit poorly with our current understanding of urban ecosystem 65 66 functioning. For many urban animals, key resources are inextricably linked with human culture, an aspect that has been largely overlooked. 67 68 69 **Keywords:** human culture; human subsidies; nest availability; population limitation; 70

- 71 tree management; urban raptor
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Urbanization is one of the most rapidly expanding land uses worldwide (United Nations 73 74 2014, Malakoff et al. 2016), with profound consequences for animal individuals, populations and communities (Marzluff et al. 2008, Gaston 2010, Niemelä 2011). As a 75 result, research in urban ecology is in rapid expansion (e.g. Niemelä 2011), but three 76 aspects have received very limited attention. First, current knowledge is heavily biased 77 towards urban systems of Europe and North America, despite the fact that a major share 78 of urban sprawl is taking place in tropical countries (Grimm et al. 2008, Malakoff et al. 79 2016) and that these may present profoundly different human and ecological settings 80 from their temperate counterparts. Thus, there have been many calls highlighting the 81 urgent need for more studies from tropical cities, but with limited progress (e.g. Magle 82 et al. 2012, Mazluff 2016). Secondly, despite the fact that humans are, for obvious 83 reasons, the dominant species in the urban ecosystem, few studies have incorporated 84 85 explicit human socio-cultural aspects in their research. Such factors are increasingly recognized as essential components of the urban ecosystem, leading to an urgent need 86 87 for more insight into their ecological consequences (Shochat et al. 2006, Alberti et al. 2003, Alberti 2008). In particular, while some studies have reported biodiversity, or 88 individual-level behavioral responses by urban animals to human socio-cultural factors 89 (e.g. Kinzig et al. 2005, Kumar et al. 2018b), it is virtually unknown whether these 90 translate into population-level consequences. Thirdly, while much research has focused 91 on the relationship between animal abundance and urbanization, this has been framed 92 mainly as: (1) comparisons of population density between urban and rural sites; or (2) 93 evaluations of the landscape predictors of density measured within small vegetation 94 patches (e.g. parks) embedded within the urban matrix of impervious surfaces (reviews 95 in Marzluff et al. 2008, Gaston 2010, Niemelä 2011). In the latter case, the small size of 96 97 these fragments enforced that density could only be studied for small-bodied species, such as many songbirds. Both these approaches are obviously valuable to tackle the 98 factors that allow certain species to colonize or persist in urban environments, but miss 99 100 important information on: (1) density variations within the urban matrix and within the fully urban core of a city landscape, which is still typically heterogeneous (Forman 101 102 2014) and could impose further internal variations in density; and (2) density variations 103 of wide-ranging species, such as raptors, whose populations may respond to integrated 104 components of the landscape that include both the urban matrix and its embedded 105 patches of "natural" habitats, but may not fit well a simplistic classification such as 106 urban vs rural.

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Thus, there is a need for studies from tropical areas that investigate whether the 107 108 density of wide-ranging species capable of urban colonization responds to variation in 109 urban configuration and human socio-cultural factors. To fill this gap of knowledge, here we examine how the population abundance of a raptor, the Black kite *Milvus* 110 *migrans*, breeding in a tropical megacity responds to variation in landscape features and 111 human cultural factors that mediate food and nest-site availability. 112 Raptors are upper-trophic-level, wide-ranging predators. Many species of this avian 113 group have recently been shown to be able to colonize and even thrive in urban areas, 114 115 by attraction to abundant prey supplies usually directly or indirectly promoted by human subsidies (Boal & Dykstra 2018). Raptor populations are typically limited by 116 117 food and nest sites (Newton 1979), both of which are likely to depend in urban areas on 118 structural landscape features and human socio-economic processes. However, it is 119 virtually unknown whether the population levels of these species vary among different 120 types of urban configuration, or in response to human cultural factors. Such a lack of 121 knowledge is likely caused by the low density of these species and the consequent challenges to survey enough study areas of sufficient size to investigate variations in 122 123 density and link them to urban features.

124

125 Methods

126 *Model species*

The Black kite (hereafter "kite") is a medium-sized, opportunistic predator and 127 facultative scavenger. In India, the resident subspecies M. m. govinda is synurbic 128 (Francis & Chadwick 2012), i.e. it occurs almost exclusively in close association with 129 humans in towns and cities (Naoroji 2006). In Delhi, where this study was conducted, 130 kites breed throughout the city, often a few meters from human habitation, thanks to the 131 132 exploitation of human food subsidies facilitated by inefficient refuse disposal and by religious kite-feeding practices (Fig. 1, Kumar et al. 2014, 2018a; see details below). 133 134 While kites over-select breeding-sites with ready access to such subsidies (Kumar et al. 2018a), it is currently unknown whether this generates heterogeneity in breeding 135 distribution at the population level, especially once controlling for nest-site availability. 136 Overall, the large area of this megacity and the magnitude of its food subsidies for kites 137 138 generate one of the largest raptor concentrations of the world (Kumar et al. 2014). In turn, this offers a unique opportunity to examine how a predator population density 139

varies among city-sectors which differ in access to religious subsidies, landscapeconfiguration and availability of nesting structures.

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143 *Study Area*

144 Delhi is a megacity of more than 16 million inhabitants, covering an area of 1500 km² and in constant expansion (http://censusindia.gov.in/2011census). Three aspects of 145 Delhi are important for kites. First, much of the city is characterized by poor solid waste 146 management, which affords plenty of food to kites in the form of carrion or refuse. 147 148 Secondly, many people engage in the centuries-old religious practice of feeding meat scraps to kites (hereafter termed 'ritualized-feeding'), typically offered by throwing 149 150 meat into the air for the birds to catch (Fig. 1). These offerings are made for a variety of 151 reasons, such as asking for blessings and relief from sins and worries (Pineault 2008, 152 Taneja 2015). Whilst meat-offering is practiced by a number of communities, in Delhi it is especially prevalent amongst members of the Islamic faith, whose numbers are 153 154 concentrated in well-defined portions of the city (hereafter 'Muslim colonies') where large quantities of meat are tossed to kites at predictable hours each day, sometimes 155 156 causing hundreds of kites to congregate. Third, Delhi still retains reasonable green 157 cover, thus providing abundant nesting habitat for kites (Paul and Nagendra 2015). However, tree cover is also being rapidly lost (Paul and Nagendra 2015), which calls for 158 159 the need to forecast the potential ecological consequences of such changes.

160

161 *Field procedures*

We surveyed kite nests systematically in 2013-2018 at 28 plots of approximately 1 km². 162 These were plotted randomly within Delhi (1500 km²) so as to cover all its possible 163 urban settings, from semi-natural to extremely built-up sites (details in Kumar et al. 164 165 2014). We surveyed each plot by walking slowly and carefully inspecting all potential nest structures (trees, poles, towers etc.). Structures were classified as active nest-sites 166 167 when a kite individual or pair was observed to perch on a nest or its immediate surroundings, or to add material to a nest. Each plot was surveyed \geq three successive 168 times each year during the breeding season, separated by ≥ 20 days until we were 169 reasonably confident to have detected all territorial pairs. This generated an overall 170 171 sample of 79 plot-years available for analysis. To measure nest-site availability for each 172 plot, we: (1) digitized all large-enough trees clearly visible in Google Earth imagery; (2) 173 visited each plot and mapped any additional trees that were not visible in Google Earth

174 (e.g. because of low quality, blurred imagery for some sectors of Delhi) and all potential

anthropogenic nest-structures (e.g. poles, towers) that were typically too difficult to

detect in Google Earth. Because more than 90 % of the available nest-structures were

trees, we summed trees and artificial structures into a single cumulative estimate of

- 178 breeding-site availability.
- 179

180 *Statistical analyses*

To investigate the predictors of kite population-density, for each plot we collected a 181 182 number of landscape and human variables (Table S1) chosen on the basis of our knowledge of kite ecology and of previous analyses of the factors that affect habitat 183 184 preferences, breeding success and behavioural performance by Delhi kites (Kumar et al. 185 2018a,b, 2019). These variables characterized each plot in terms of its landscape 186 structure, food availability (e.g. local availability of organic garbage, access to Muslim ritual-subsidies), and nest-site availability (details in Table S1). We further 187 188 hypothesized that the effect of food availability could interact with nest availability in shaping density (e.g. Newton 2013) and thus also modelled the interaction of nest 189 190 availability with Muslim subsidies or with refuse availability. We then tested the effect 191 of the above variables on kite density as follows. Because density could be spatially 192 autocorrelated, we initially modelled it through a spatial linear mixed model by means of a Bayesian approach, as outlined in Zuur et al. (2017). However, such a model gave 193 poor support to the presence of spatial autocorrelation and gave the same conceptual 194 results (Appendix S1). Thus, we repeated the analysis by means of a linear mixed model 195 (LMM) with normal errors and an identity link (Zuur et al. 2009), where plot-identity 196 was fitted as a random factor. The LMM was built through a backward stepwise 197 procedure following Zuur et al. (2009): all explanatory variables were fitted to a 198 199 maximal model, extracted one at a time, and the associated change in model deviance was assessed by the significance of a likelihood-ratio test; the procedure was repeated 200 201 until we obtained a final model which only included significant variables (Zuur et al. 2009). The R² of the LMM was calculated following Nakagawa and Schielzeth (2013). 202 203 Variables were standardized before fitting them to the models and all analyses were performed through R 3.4.3 (R Development Core team 2017). 204

- 205
- 206 **Results**

The average density in Delhi was 19.02 breeding pairs/km² (SE = 7.43, n = 28 independent plots). Kite density increased with deteriorating sanitation levels (i.e. more human refuse in the streets) and depended on the interaction between access to Muslim subsidies and nest-site availability (Table 1): density increased more steeply with Muslim subsidies when breeding sites were abundant than when they were in poor supply (Fig. 1). These explanatory variables explained 89.9 % of the variation in density.

214

215 **Discussion**

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217 Kite density was tied to spatial variation in human subsidies, in the form of human refuse, ritual offerings and their ready accessibility. Because kite breeding pairs were 218 219 previously shown to select sites with these same characteristics (Kumar et al. 2018a), 220 individual-level habitat selection scaled up to population-level consequences. However, 221 the subsidy-effect on density was more complex, because it was also modulated by breeding-site availability. Higher nest-site availability allowed the population to 222 223 increase more steeply and reach higher densities in response to religious subsidies (Fig. 224 1). Conversely, lower nest availability constrained the breeding population to a weaker response to religious subsidies (Fig. 1). Thus, the availability of nesting structures 225 226 modulated the capability of the population to track its food resources. As a 227 consequence, only the combination of high availability of both human subsidies and urban nesting structures (trees, artificial poles and towers) allowed the population to 228 reach the extremely high densities that generate what is probably the largest raptor 229 230 concentration in the world. The above results are important for two reasons. First, most of the support for the 231

232 limitation of animal populations by breeding site availability is given by experimental studies based on nest-box addition-removals (reviews in Newton 1998, 2013). For 233 234 species that build their own nests, demonstrations of the importance of nest availability are scarcer, probably because measuring the availability of nesting structures is often 235 236 difficult or very time consuming. In urban settings in particular, we are not aware of previous studies showing links between population density and breeding-site 237 238 availability, despite their obvious importance for management in the highly "engineered" landscape of urban ecosystems. Secondly, while the importance of human 239 240 subsidies for predator populations is well established (e.g. Oro et al. 2013, Newsome et

al. 2014), the fact that breeding-site availability can mediate their population-effect is,
to our knowledge, reported here for the first time, and could be exploited for
management purposes (see below).

Overall, our results showed how the density of an urban raptor was limited by food 244 and nest-sites, whichever was in shorter supply. This suggested the action of processes 245 of population functioning in urban settings broadly similar to those observed in more 246 natural habitats (e.g. Newton 1997, 1998, 2013), but their modality and underlying 247 mechanism stood out strikingly in that food was dictated by the spatial zoning of human 248 249 socio-religious and cultural practices. This stresses the importance of human behaviours 250 and culture as an interactive component of the urban ecosystem (Alberti 2008). In fact, 251 for synanthropic species that have closely coexisted with man in cities for centuries and 252 are thus in the mature stages of urban colonization, humans can become a targeted 253 resource and the leading component of their ecological niche, rather than a constraint to 254 avoid or withstand. For example, in our population more than 90 % of the diet was 255 dominated by ritual subsidies (unpubl. data from > 1000 prey items from camera-256 trapping at 40 nests).

257 To date, other studies have reported the effect of human socio-economic factors on the behaviour of the individuals of certain species (e.g. van Heezig and Hight 2017, 258 Kumar et al. 2018b) or on the biodiversity of gardens and parks embedded in the urban 259 260 matrix (e.g. Kinzig et al. 2005, van Heezig et al. 2013). Here, we show that these individual and local effects can scale-up to population-level responses. This highlights 261 how human practices and culture, which are often spatially clustered in cities for socio-262 economic and historical reasons (Kinzig et al. 2005), can structure the urban landscape, 263 264 ultimately creating ecologically-relevant social gradients which are independent and 265 overlaid over more classical gradients based on urban physical structures (e.g. housing 266 density) or position along an urban-rural transition. Such socio-cultural gradients are often challenging to detect and to measure, because they may not be reflected by any 267 268 strikingly visible or physical feature (Faeth et al. 2005). However, the fact that their modelling explained nearly 90 % of the variation in kite density and that diet was so 269 270 dominated by religious offerings provides compelling support for the often stressed 271 need to incorporate a sociological perspective into studies in urban ecology (Grimm et 272 al. 2008, Alberti et al. 2003, 2008, Marzluff et al. 2008). In particular, we emphasize 273 that socio-economic and cultural gradient is likely to be present in most cities of the 274 world. In the much studied cities of Europe and North America, such gradients often

reflect differences in income and social status (e.g. Kinzig et al. 2005), while our study 275 276 completes this picture by showing gradients based on religious factors, sanitary 277 conditions and refuse management. These latter types of gradients are likely to be 278 commonplace over large portions of southern Asia, Africa and South America, where most of the urban growth is currently concentrated (Malakoff et al. 2016). In many of 279 280 these regions, poor sanitary conditions in urban areas promote social acceptance of species that offer ecosystem services through refuse consumption, such as many 281 scavengers (Campbell 2009, Barlow and Fulford 2013, Gangoso et al. 2013, Bildstein 282 283 and Therrien 2018). Because sanitary conditions are usually tied to poverty, which is 284 typically heterogeneously distributed within cities (Kilroy 2009), the stage is set for 285 socially-generated variation in subsidies and resources, as well as human perceptions and responses to wildlife. Finally, the effect shown here of socio-cultural factors on 286 287 wildlife populations implies that geographic variation in human cultural aspects can generate marked variation in the basic functioning of urban ecosystems from different 288 289 regions. This stresses the urgency of completing our views of urban ecology through more studies on the strongly overlooked cities of the so-called developing world. 290

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292 Implications for management and conservation

Interestingly, both the factors that seemed to limit the kite population (food and 293 294 breeding-sites) were already directly or indirectly managed by humans. In particular, 295 nest availability could easily be exploited through tree addition or removal in order to increase or constrain local predator density. For example, density could be enhanced 296 close to urban areas with poor sanitation infrastructures in order to boost the ecosystem 297 service function of kites, while density could be reduced in areas with conflictive pairs 298 that attack humans for nest defence or to steal food (Kumar et al. 2019). Because urban 299 300 ecosystems are typically temporally dynamic, a good understanding of the factors underlying local abundance is key to forecast or minimize the future impacts of such 301 302 changes. For example, urban development in Delhi is currently causing rapid and often dramatic erosion of tree-cover (Paul and Nagendra 2015). This could cause a 303 304 progressive decline in the ecosystem service offered by kites, with potential repercussions even on human health, for example through an increase in rotting organic 305 306 waste or in populations of feral dogs. The latter are a major source of rabies for humans 307 in India and have been shown to increase in response to declines of scavenging birds 308 (Markandya et al. 2008).

9

309		In conclusion, human socio-cultural factors may represent a widely overlooked force		
310	in u	urban ecology and conservation, and their impact may be even greater than currently		
311	app	ppreciated in the poverty-structured cities of the developing world, where social		
312	ine	inequalities and cultural beliefs may be tied to human subsidies and wildlife		
313	per	perceptions. The massive food-base so generated may have population impacts further		
314	mo	dulated by anthropogenic structures that provide safe breeding, roosting and resting		
315	site	s, whose availability could be easily exploited as a management tool. Thus, for many		
316	urb	an animals key resources are inextricably linked to human culture.		
317				
318	Ac	knowledgements		
319				
320	We	thank Ujjwal Kumar and the Director of the Wildlife Institute of India for materials		
321	and	advice on various aspects of the project. We thank Laxmi Narayan, Prince Kumar,		
322	Рос	onam and all the "Black Kite Project Group" for help in the field.		
323				
324	Fu	nding		
325	Thi	s work was supported by the Raptor Research and Conservation Foundation		
326	(Mumbai) and by the Govt. of India, Ministry of Environment, Forest and Climate			
327	Cha	ange.		
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329	Re	ferences		
330	1.	Alberti M. 2008. Advances in urban ecology: integrating humans and ecological		
331		processes in urban ecosystems. Springer, New York.		
332	2.	Alberti MJ, Marzluff M, Schulenberger E, Bradley G, Ryan C, Zumbrunnen C.		
333		2003. Integrating humans into ecology: opportunities and challenges for studying		
334		urban ecosystems. BioScience 53, 1169-1179.		
335	3.	Bildstein K.L, Therrien J-F. 2018. Urban birds of prey: a lengthy history of		
336		human.raptor cohabitation. Pages 3-17 in C.W. Boal, and C.R. Dykstra, editors.		
337		Urban raptors: ecology and conservation of birds of prey in cities. Island Press,		
338		Washington DC.		
339	4.	Boal CW, Dykstra CR. 2018. Urban raptors: ecology and conservation of birds of		
340		prey in cities. Island Press, Washington DC.		

341	5.	Barlow C.R, Fulford T. 2013. Road counts of Hooded Vultures Necrosyrtes
342		monachus over seven months in and around Banjul, coastal Gambia, in 2005.
343		Malimbus 35 , 50–56.
344	6.	Campbell M. 2009. Factors for the presence of avian scavengers in Accra and
345		Kumasi, Ghana. Area 41.9 , 341–349.
346	7.	Faeth SH, Warren PS, Shochat E, Marussich WA. 2005. Trophic dynamics in urban
347		communities. BioScience 55, 399-407.
348	8.	Forman, R. T. T. 2014. Urban ecology: science of cities. Cambridge University
349		Press, Cambridge, UK.
350	9.	Francis RA, Chadwick MA. 2012. What makes a species synurbic? Applied
351		<i>Geography</i> 32 , 514-521.
352	10.	Gangoso L, Agudo R, Anadón JD, de la Riva M, Suleyman AS, Porter R, Donázar
353		JA. 2013. Reinventing mutualism between humans and wild fauna: insights from
354		vultures as ecosystem services providers. Conservation Letters 6, 172-179.
355	11.	Gaston KJ, editor. 2010. Urban ecology. Cambridge University Press, Cambridge,
356		UK.
357	12.	Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM.
358		2008. Global change and ecology of cities. Science 319, 756-760.
359	13.	Kilroy A. 2009. Intra-urban spatial inequality: cities as "Urban Regions". World
360		Bank, Washington, DC. https://openknowledge.worldbank.org/handle/10986/9144.
361	14.	Kinzig AP, Warrren P, Martin C, Hope D, Madhusudan K. 2005. The effects of
362		human socioeconomic status and cultural characteristics on urban patterns of
363		biodiversity. Ecology and Society 10, 23.
364	15.	Kumar N, Gupta U, Jhala YV, Qureshi Q, Gosler AG, Sergio F. 2018a. Habitat
365		selection by an avian top predator in the tropical megacity of Delhi: human
366		activities and socio-religious practices as prey-facilitating tools. Urban Ecosystems
367		21 , 339-349.
368	16.	Kumar N, Qureshi Q, Jhala YV, Gosler AG, Sergio F. 2018b. Offspring defense by
369		an urban raptor responds to human subsidies and ritual animal-feeding practices.
370		PLoS ONE 13(10): e0204549. https://doi.org/10.1371/journal.pone.020454
371	17.	Kumar N, Jhala YV, Qureshi Q, Gosler AG, Sergio F. 2019. Human-attacks by an
372		urban raptor are tied to human subsidies and religious practices. In press in:
373		Scientific Reports.

18. Kumar N, Mohan D, Jhala YV, Qureshi Q, Sergio F. 2014. Density, laying date, 374 375 breeding success and diet of Black kites *Milvus migrans govinda* in the city of 376 Delhi (India). Bird Study 61, 1-8. 377 19. Magle SB, Hunt VM, Vernon M, Crooks KR. 2012. Urban wildlife research: past, present, and future. Biological Conservation 155, 23-32. 378 379 20. Malakoff D, Wigginton NS, Fahrenkamp J, Wible B. 2016. Rise of the urban planet. Science. doi:10.1126/science.aaf5729. 380 21. Markandya A, Tayor T, Longo A, Murty MN, Murty S, Dhavala K. 2008. Counting 381 382 the cost of vulture decline - an appraisal of the human health and other benefits of 383 vultures in India. Environmental economics 67, 194-204. 384 22. Marzluff JM. 2016. A decadal review of urban ornithology and a prospectus for the 385 future. Ibis 159, 1-13. 386 23. Marzluff JM et al., editors. 2008. Urban ecology: an international perspective on the interaction between humans and nature. Springer Science, New York. 387 388 24. McKinney ML. 2010. Urbanization, biodiversity, and conservation. BioScience 52, 883-890. 389 390 25. Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R² 391 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4, 392 133-142. 26. Naoroji R. 2006. Birds of prey of the Indian subcontinent. OM Books International, 393 Noida, India. 394 27. Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, 395 Dickman CR. 2014. The ecological effects of providing resource subsidies to 396 397 predators. Global Ecology and Biogeography 24, 1-11. 28. Newton I. 1979. Population ecology of raptors. T & AD Poyser, Berkhamsted, UK. 398 399 29. Newton I. 1998. Population limitation in birds. Academic Press, London. 30. Newton I. 2013. Bird populations. HarperCollins, London. 400 401 31. Niemelä J, editor. 2011. Urban ecology: patterns, processes and applications. Oxford University Press, Oxford, UK. 402 32. Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A. 2013. 403 Ecological and evolutionary implications of food subsidies from humans. *Ecology* 404 405 Letters 16, 1501-1514. 33. Paul S, Nagendra H. 2015. Vegetation change and fragmentation in the mega city 406 407 of Delhi: mapping 25 years of change. Applied Geography 58, 153-166.

408	34.	Pinault D. 2008. Raw meat skyward: Pariah-kite rituals in Lahore. Pages 108-121
409		in D. Pinault, editor. Comparative Islamic studies: notes from the fortune-telling
410		parrot: Islam and the struggle for religious pluralism in Pakistan. Equinox
411		Publishing Ltd, London.
412	35.	R Development Core Team. 2017. R: A language and environment for statistical
413		computing. R Foundation for Statistical Computing, Vienna.
414	36.	Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D. 2006. From patterns to
415		emerging processes in mechanistic urban ecology. Trends in Ecology and Evolution
416		21 , 186-191.
417	37.	Taneja AV. 2015. Saintly animals: the shifting moral and ecological landscapes of
418		North India. Comparative Studies of South Asia, Africa and the Middle East 35,
419		204-221.
420	38.	United Nations. 2014. World urbanization prospects: the 2014 revision highlights.
421		United Nations, New York.
422	39.	van Heezig Y, Freeman C, Porter S, Dickinson KMJ. 2013. Garden size,
423		householder knowledge, and socio-economic status influence plant and bird
424		diversity at the scale of individual gardens. Ecosystems 16, 1442-1454
425	40.	van Heezig Y, Hight SR. 2017. Socio-economic-driven differences in bird-feeding
426		practices exacerbate existing inequities in opportunities to see native birds in cities.
427		Journal of Urban Ecology 2017, 1-7. doi: 10.1093/jue/jux011.
428	41.	Zuur AF, Ieno EN, Saveliev AA. 2017. Spatial, temporal and spatial-temporal
429		ecological data analysis with R-INLA. Volume I: using GLM and GLMM. Highland
430		Statistics, Newburgh, UK.
431	42.	Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects

432 *models and extensions in ecology with R.* Springer, New York.

433 Table 1. Linear mixed model with normal errors and an identity link function testing the

434 effect of landscape and human variables on the population density of Black kites in the

435 megacity of Delhi (India).

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Variable	$B \pm SE$	t	Р
		1 40	0.166
Access to Muslim subsidies	6.07 ± 4.25	1.43	0.166
Refuse availability score	16.18 ± 6.80	2.38	0.025
Nest-site availability	29.87 ± 5.57	5.36	< 0.001
Access to Muslim subsidies * Nest-site availability	13.10 ± 4.90	2.67	0.010
Intercept	13.19 ± 3.53	3.74	0.010

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Fig. 1. The Black kites of Delhi depend heavily on human subsidies offered for religious reasons: (a) a man with his two sons ritually feeds kites with the typical, compact chunks of red meat (red circle); (b) large numbers of kites, sometimes into the hundreds, may congregate at such feeding events; (c) the ritual offerings are taken to the nests; (d) a parent kite is about to feed its fledgling with a ritual meat chunk. More than 90 % of the diet in this population is composed of ritual offerings, which explains the tight link between breeding density and ready access to human cultural subsidies (Photo credit for all images: F. Sergio).

Fig. 2. The population density of Black kites in the megacity of Delhi (India) increases with food availability (access to Muslim subsidies), but such relationship is modulated by the availability of breeding-sites. For clarity of visualization, nest availability is here depicted as high (above the median value of nest availability: black dots, continuous line) or low (below the median value: white dots, hatched line).



Access to Muslim subsidies

Table S1. Landscape and human variables used to characterize each study plot in which we surveyed the population density of Black kite breeding pairs within the city of Delhi (India). Variables were chosen on the basis of our knowledge of kite ecology and of previous analyses of the factors that affect habitat preferences, breeding success and behavioural performance by Delhi kites (Kumar et al. 2018a,b, 2019). These variables characterized each plot in terms of its landscape structure, food availability (local availability of organic garbage, access to Muslim ritual-subsidies, local density of humans walking in the streets), and nest-site availability. See the Study Area section for background details on the rationale underlying the choice of indicators of human refuse and ritual subsidies.

Variable	Description
Nest-site availability	Density (number/km ²) of structures potentially capable to support a kite nest, such as trees of sufficient height, or anthropogenic structures such as pylons and towers (Kumar et al. 2018a). For each plot, we: (1) digitized all large-enough trees clearly visible in Google Earth imagery; (2) visited each plot and mapped any additional trees that were not well visible in Google Earth (e.g. because of low quality, blurred imagery for some sectors of Delhi, or because of the shadow produced by tall buildings) and all potential anthropogenic nest-structures (e.g. poles, towers) that were typically too difficult to detect in Google Earth. For plots in which nesting-structures were too many to count individually, we: (1) plotted 20 random locations within each plot; (2) visited them in the field and counted all nesting-structures observed in a circular buffer of 200 m radius centered on each of these 20 random locations to calculate a cumulative density of nesting structures/km ² .
	of the available nest-structures were trees, we summed trees and artificial structures into a single cumulative estimate of breeding-site availability.
Refuse availability score	Level of sanitation of the plot: 1 = clean areas (efficient waste disposal with very scarce or no organic refuse in the streets); 2 = areas under poor waste management regime (abundant and widespread refuse in the streets throughout the area, either in small frequent piles, in illegal ephemeral dumps, or as individual items scattered a bit of everywhere through all streets).
Human density	Average number of people walking within 2m of a stationary observer during 5 min at 10 locations randomly plotted within 200 m of a nest, and averaged over all nests censused in a plot. Counts were only operated between 10:00-17:00 hrs and avoided during atypical, momentary peak periods of human traffic, such as exits from work or schools in order to maintain consistency across sites (following Kumar et al. 2018a)
Access to Muslim subsidies	First component (PC1) of a principal component analysis on the density of Muslim inhabitants in the plot and on the proximity of the plot to the three closest Muslim colonies. A key variable in our previous analyses on the

	predictors of kite site selection, occupancy, breeding and behavioral performance was the ease of access to
	dense Muslim colonies, which provide abundant food supplies in the form of ritual subsidies (Kumar et al.
	2018a, b). More specifically, we previously showed that Delhi kites over-selected breeding sites closer than
	available to the 1st, 2nd and 3rd nearest Muslim colony (see Kumar et al. 2018a for details). Thus, to provide a
	comprehensive measure that integrated the proximity to the three nearest Muslim colonies with their human
	population density (under the assumption that higher rates of refuse and ritualized-feeding should occur in more
	densely-populated Muslim colonies), we extracted the first axis (PC1) of a Principal Component Analysis
	(PCA) run on these four aforementioned variables. Its PC1 (hereafter "access to Muslim subsidies") explained
	83% of the variance and had a high positive loading on Muslim population density and high negative loadings
	on the distance to the 1st, 2nd and 3rd closest Muslim colonies. Thus, it provided an increasing index of access
	to abundant "Muslim subsidies" (details in Kumar et al. 2018a).
Index of road density	Number of asphalted roads crossed by a 500 m north-south and a 500 m east-west transect crossing each other
	on a nest, and averaged over all nests censused in a plot.

Appendix S1. Spatial analysis of Black kite density

Methods

Because of potential spatial dependency, kite density was initially modelled through a spatial linear mixed model (LMM) by means of Bayesian methods, as detailed in Zuur et al. (2017). The model incorporated a Guassian Markov random field that controls for spatial dependency and autocorrelation. The estimation of the spatial random field was based on the creation of a dense triangular grid (mesh) overlaid on the study area (Fig. 1 below) to solve a "continuous domain stochastic partial differential equation" (SPDE), in turn used to calculate the parameters of the Matérn correlation function which estimates the spatial random term. The explanatory variables (see Methods and Table S1) were fitted to the model through diffuse priors, and considered as "important" when their 25 % and 95 % credible intervals did not overlap zero. Study plot identity was always fitted as a random effect. Support for inclusion of a spatial random field was examined by comparing the LMM with and without the spatial field by means of the DIC statistic. Zuur et al. (2017) suggest a Δ DIC > 10 units to provide support for a model over another. All model building and checking procedures follow Zuur et al. (2017).



Fig. 1. Mesh overlaid on the Delhi study area to estimate the spatial field fitted to the linear mixed model used to relate kite density to explanatory variables. The mesh was based on a grid of > 4000 triangle-vertices (4299), following recommendations by Zuur et al. (2017). The black circles represent the kite study plots.

Results

Two variables appeared as important, as their 25 % and 95 % credible intervals did not overlap zero (see Table 1 below). These were: human density and the interaction

between Access to Muslim subsidies and Nest availability. There was poor support for the need of a spatial random field: the spatial model was only 2.78 DIC units less than the model without a spatial random field.

Table 1. Slope and credible intervals of a spatial linear mixed model testing the effect of landscape structure, food availability and breeding-site availability on the population density of an urban raptor. Important variables, whose credible intervals do not overlap zero, are highlighted in bold .

Variable	Mean	25 % credible interval	95 % credible interval
Intercept	-15.33	-44.63	14.55
Access to Muslim subsidies	-3.40	-27.08	20.35
Quadratic effect of Access to Muslim subsidies	-6.84	-18.52	4.87
Nest availability	-0.01	-0.04	0.02
Hygiene score	-1.27	-4.53	1.96
Human density	18.18	3.76	32.23
Index of road density	1.04	-1.64	3.76
Access to Muslim subsidies * Hygiene score	0.87	-0.99	2.74
Access to Muslim subsidies * Nest availability	0.01	0.01	0.03



Our Feathered Co-inhabitants of Delhi

Coexisting migrant and resident Black Kite races in a developing megacity



भारतीय वन्यजीव संस्थान Wildlife Institute of India


Oh Yeah ! a janitor's worth is established only on absence from duty. Poor Wiltures ! [SIGH]

Birders know me as Lineatus, Call me Linn.

Odelhikites

If you're a lay / city person, you probably know us as Eagles !





Short goon I'm, O' Russian visitor, I munch on feeding rituals, as a city scavenger.



Odelhikites

I'm all streaky, with more roufous coat, sporting yellow tarsi, you seem light and short!

Black-eared is what i am called, with a white carpel patch. While we feast on landfill offal your adaptations have no match.

Hand-in glove with Indians, religiously i evolved.. Share your story in elaboration, when the reader is on hold.













We have been doing "steeplechase" across Chinese highlands, deserts, and the mighty Trans- Himalayas, for millions of years, before you humans left Africa.

Bishkek - Issyk Kul

Hashkent

South Kazakhstan

ushânbe

Odelhikites

Jammu and Kashmir

Haryar

Islamabac

Punjab region

Jambyl

Leh

Punjab Himachal Pradesh Chandigarh Uttarakhand

New Delhi

naken Deserit

Far-Western

But in mere 300 Years, our favourite wintering grounds have been riddled by your enormous cilies.

Too fast a change you see !

CHINA ?

Mid-Western

Nepal







In the region you stand and read about us, we annually meet our old cousins, the Govinda kites.

Evidently, these "architects' build cities for their folks. As facultative scavengers, we adaptively nest near them and pretty much snatch morsels from their hands

we have to suffice on

What all one goes through to be a parent, post winter.

Hmm., thankfully, Delhites (Muslims) ritually offer us meat chunk subsidies. We teem and nest in their city parks and woodlots to capitalize, and yield to become

the commonest raptors.

SI

Unassuming, as "immigrants"

their predictable garbage and offall













But as the saying goes, Nothing is Free ! We wonder about the consequences of their " urban fast food " : Toxic metals, bioaccumulation, etc. is what i read on Google.



Don't forget its consequence to our inner worlds : "the microbiome". Some of the readers would recall my range. It coincides with the hot spots of bird flu in China.





Yeah! Our new neighbours, a lazy nesting couple; they lost their chicks to perpetual meat chunk diet. The pale appearance and bone deformities of chicks were scary.







© delhikites

Add to it the expected preparedness for the months you guys are not here. Relentless garbage accumulation will only yield aircraft collisions, and higher likelihood of

You are right ! Homogeneity in cities physical structure, and social fabric will make my upcoming vacation rather boring.



Affirmative ! Unless the younger generation picks the walking boots to crusade against extinction of experience, we won't even find place in their folklores.

Google US @

1. Density, laying date, breeding success and diet of Black Kites Milvus migrans govinda in the city of Delhi (India). 2. Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and Socio-religious practices as prey-facilitating tools 3. Raptors associated with airports and aircraft. In the book: Raptors in human landscapes: adaptations to built and cultivated environments: Page # 315-323. 4. https://delhikites.wixsite.com/121212





Small Indian Kite (Milvus migrans govinda) ©F. Sergio





Black-eared Kite (Milvus migrans lineatus) ©L. Narayan













दिल्ली के सह-निवासी पक्षी

जानिए अपनी निवासी व प्रवासी चीलों को

©delhikites

LINN.

CA.

भारतीय वन्यजीव संस्थान Wildlife Institute of India



ईगल? पता नहीं ये 'सभ्य' शहरी हमें और किन-किन नामों से पुकारेंगे !

बिलकुल ! अब इन्हें गिद्ध याद आ रहे है ? प्रकृति के सफाई कर्मचारी आज की पीढ़ी के लिए "रामू काका" रह गए है | बेचारे गिद्ध !

अंग्रेजी में मुझे lineatus कहते है | वैसे 'लिन' उपनाम कैसा रहेगा?

Odelhikites

हाँ भाई, चीनी परिवेश का असर तोह पड़ेगा ही! लिन :) मैं पूरा गंगा घाट वाला देसी, मिलवस मिग्रेंस गोविंदा हूँ। हाव-भाव, चाल-ढाल, ओह गोविंदा!



अरे, हमें तो ये गिद्ध कौवा, गौरैया और न जाने किन किन नामों से बुलाते है P. K. है का ?



धारीदार है तन मेरा, तुझसे गोरा रंग | पतली, पीली सूखी टॉॅंगे, तू छोटा- हल्का बेढंग |

רואא.

छोटा हूँ, पर बड़े काम का, सुन रूसी मेहमान | सड़ा−गला खाकर करता, सड़के साफ़ तमाम|

> काली कनपटी वाला मैं, पंख के नीचे सफ़ेद | मैं भी कूड़ा जम कर खाता, तू बता अब अपना भेद |

हाथ मिलाकर देसी लोगों से, बढ़ी है मेरी शान |ध्यान खींच अपने पाठक का, खुलकर बता अपनी पहचान |

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Haryar

New Delhi

Odelhikites

Uttarakhand

Far-Western

हालांकि महज ३०० सालों के तुम्हारे शहरीकरण ने हमें पलायन के रास्ते में कई बार भटका दिया है| महज ३०० साल!

Kuthun Mountains

-

Mid-Western-Nepal

Kathmandu Central

_aste

Tibetan Plate



Odelhikites

करने की लिए बनते हैं |

हाँ यार, पर पुरानी दिल्ली के बाशिव्दे हमें सदियों से गोश्त छिछड़े खिलाते आये हैं |इस्लाम में इसे चील का सदक कहते हैं , यह मानते हुए कि हम

इनके लिए तो हम तुच्छ पक्षियों का एक झुण्ड है, जो कुड़े के ऊपर मंडराता है | इन्हें क्या खबर कि हम प्रवासी चीलें यह सब मात्र बेहतर प्रजनन

भई, हम सभी तो इनके शहरों में पुरे ढल चुके है | कई बार तो हम मौक़ापरस्त, इनके हाथों

और एक बात तो सभी भूल जातें हैं :- इस मुफ्तखोरी और शहरीकरण का हमारे सूक्ष्म -जैव विविधता पर क्या असर होगा | वैसे चीन में हमारी वितरण रेंज घातक 🕻 बर्ड-फ्लू वाले इलाके से जुडी है |

©delhikites

जैव-संचयन



पर भई, मुफ्त का चन्दन कब तक घिस सकते हैं ? वो तो अच्छा है कि तुम भी हमारी तरह प्रजनन के समय आवश्यकतानुसार ताज़ा शिकार कर लेते हो | मैं तो बस इंसानी बस्तियों के कूड़े वाले लंगर को लेकर चिंतित हूँ | गुगल पर ऐसी मुफ्त खोरी के गंभीर परिणाम बताये गए हैं :- विषैली धातु, जैव-संचयन आदि





यार तुम्हारी चिंता सौ टके ठीक है | अब हमारे पड़ोसी घोंसले वाले नए गोंविदा जोड़े को ही ले लो | छिछड़ों पर मुफ्तखोरी कि वजह से उनके बच्चे निकल लिए | कुपोषित, टेढ़ी हड्डियों देख कर दुया आ रही थी |





Odelhikites

बना देती है |

एकदम सही | अरे मैं तो कहता हूँ, कि समय रहते नौजवान और आनेवाली पीढ़ियाँ अगर खुले में **प्रकृति** से रू-बरू होते रहे, तो शायद हम भी **गिद्धों** के साथ साथ इनके किस्सों से भी विलुप्त हो जाएंगे |



Small Indian Kite (Milvus migrans govinda) ©F. Sergio



Google vs @

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